

Black-backed Woodpecker Resource Selection and Demographic Responses to Variation in Fire Characteristics

Andrew N. Stillman, PhD
University of Connecticut, 2021

Wildfire is an agent of change in forested landscapes worldwide, creating challenges and opportunities for wildlife. Variation in fire regime characteristics – termed pyrodiversity – plays an important role in structuring post-fire communities. However, little is known about the ways individual species respond to pyrodiversity and use the ephemeral resource patches created by fire. My dissertation research addresses two questions in post-fire landscapes: How do animals use and react to temporary resource pulses after fire? How do animals respond to variation in post-fire landscapes? I investigate hypotheses related to resource selection, behavior, and demography with a focus on a post-fire specialist bird, the black-backed woodpecker (*Picoides arcticus*). I begin by employing a combination of field observations, radio-telemetry, and ecological modeling to assess how black-backed woodpeckers respond to fire characteristics and post-fire resource pulses. I show that black-backed woodpeckers exhibit age-specific habitat relationships largely driven by tradeoffs between foraging and predation risk. Adult woodpeckers use resource-rich areas that burned at high severity while fledglings primarily use areas that burned at low severity, where live trees provide cover from predators. Moreover, I show that black-backed woodpeckers exhibit natal dispersal strategies that enable populations to follow unpredictable and temporary pulses of food and habitat created by fires in the western U.S. Last, I use molecular approaches to characterize the arthropod diets of four woodpecker species in burned areas to understand how they use the food sources available after fire. This dissertation work highlights the importance of pyrodiversity for animals that thrive in post-fire habitat and

demonstrates how fire-associated species can locate and track patchy, ephemeral resources after fire. In addition, this research advances our knowledge of the complex and nuanced relationships between biodiversity and fire while providing important insights for land managers tasked with responding to emerging socio-ecological challenges in fire-prone landscapes.

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Variation in Fire Characteristics

Andrew N. Stillman

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Doctor of Philosophy Dissertation

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Variation in Fire Characteristics

Presented by

Andrew N. Stillman, B.S.

Approved by

Major Advisor: Morgan W. Tingley

Associate Advisor: Chris S. Elphick

Associate Advisor: Tracy A.G. Rittenhouse

Associate Advisor: J. Michael Reed

University of Connecticut
2021

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Dedication

This PhD dissertation is dedicated to Dr. Eldridge Adams in celebration of his life and contributions to ecology.

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Introduction

Wildfire is a key disturbance event in many terrestrial ecosystems, and fire has been proposed as a major driver of landscape heterogeneity and biological diversity (He et al., 2019; Kelly et al., 2020). Fire events contribute to the dynamic nature of landscapes by resetting successional states and altering the spatial configuration of biological communities over time (Bond & Keeley, 2005; Kelly & Brotons, 2017; Pausas & Bond, 2020). Wildfire regimes are characterized by the frequency, extent, seasonality, and severity of fire (Hempson et al., 2018), and these traits can be used to classify fire-dominated ecosystems globally (Archibald et al., 2013). Individual fires can create discrete patches of post-fire habitat that are ecologically distinct from pre-disturbance states and host unique communities of plants and animals (He et al., 2019). At large spatial scales, the combination of intermittent fires followed by subsequent ecological succession can lead to a shifting patch mosaic of habitat types (Hastings, 2003; Moloney & Levin, 1996; Wimberly, 2006). Some species are highly associated with post-fire conditions (Fontaine & Kennedy, 2012; Hutto, 2008), but these ephemeral habitats present unique ecological challenges: they are temporary, patchy, and often spatially unpredictable. Post-disturbance succession gradually alters recently burned habitat over a continuum of ecological states, and different burn severities exhibit divergent responses to succession over time (DellaSala et al., 2014; Tingley et al., 2016).

Just as environmental heterogeneity is linked to greater biodiversity (Stein et al., 2014), variation in fire regime characteristics – termed pyrodiversity – can have profound impacts on the structure and function of ecological communities (He et al., 2019; Martin & Sapsis, 1992). Pyrodiversity occurs along multiple axes of variation including fire severity, seasonality, patch size, and time since fire (Bowman et al., 2016), and the belief that pyrodiversity can promote

biodiversity has become an influential principle guiding the management of fire-prone landscapes (Kelly & Brotons, 2017). In the last decade, numerous studies have provided empirical support for this pyrodiversity–biodiversity hypothesis in a variety of systems including birds and mammals in African savannahs (Beale et al., 2018) and plants, pollinators, and birds in mixed-conifer forests of western North America (Ponisio et al., 2016; Tingley et al., 2016). In these systems, pyrodiversity is expected to enhance biodiversity based on the idea that heterogeneity in the composition and configuration of burned landscapes promotes species coexistence, each with a specific niche in the fire regime. However, the potential effects of pyrodiversity on individual species and the mechanisms driving species’ responses to fire characteristics remain largely unexplored. Accordingly, species that exhibit positive responses to pyrodiversity may provide a second, though nonexclusive, mechanism driving the relationship between pyrodiversity and biodiversity in fire-prone landscapes.

Fire may benefit individual species by creating windows of elevated resource availability for many years after a fire event, following the gradual attrition of dead trees or the shift to early successional vegetation (Grayson et al., 2019; Perry et al., 2011). These post-fire conditions show strong parallels to ecological resource pulses, defined by the temporary availability of elevated levels of food, habitat, or other population requirements that subsequently decline over time (Holt, 2008; Yang et al., 2008). Animals that specialize on resource pulses face the challenge of tracking the rise and fall of resources across space and time (Curran & Leighton, 2000; Thomas, 1994), and in fire-prone landscapes, these challenges are exacerbated by the unpredictable nature of fire events. In western North America, resource pulses after fire can arise from the sudden increase in forest canopy openings (Perry et al., 2011; Smucker et al., 2005), pulses in soil nutrients (Certini, 2005), or the increase in dead trees which additionally attract

high numbers of woodboring beetles (Ray et al., 2019). Woodboring beetle larvae act as a pulsed food source for many woodpecker species, which in turn create nest cavities that are used by secondary cavity-nesting birds and mammals (Tarbill et al., 2015). Consequently, the ability of mobile species to find, colonize, and exploit post-fire resource pulses plays a key role in structuring the biotic community that arises after fire (Brotons et al., 2005; Nimmo et al., 2019).

Often called the most fire-associated vertebrate in North America, the black-backed woodpecker (*Picoides arcticus*) colonizes burned forests rapidly after fire (Hutto, 2008; Tingley et al., 2018). Black-backed woodpeckers use areas with high densities of standing dead trees, where they forage on the larvae of woodboring beetles and excavate nest cavities in dead wood (Murphy & Lehnhausen, 1998; Tingley et al., 2018). These key resources are subject to temporal declines as dead trees decay and fall in the decade following fire (Grayson et al., 2019). Consequently, black-backed woodpecker local abundance tends to peak in early post-fire years (e.g., 3–4 years post-fire) and subsequently decline over the next 3–5 years (Saab et al., 2007; Tingley et al., 2018). Previous research has demonstrated strong associations between black-backed woodpeckers and areas burned at high severity, including relationships with foraging habitat (Murphy & Lehnhausen, 1998), home range size (Tingley et al., 2014), and selection of breeding sites (Seavy et al., 2012). In unburned forests of western North America, where dead trees are more sparse, black-backed woodpecker occupancy is relatively sporadic (Fogg et al., 2014; Tingley et al., 2020). This leads to a patchy population structure among recently burned areas, mirroring the shifting habitat mosaic created by fire. The ephemeral nature of burned-forest resources and the species' sensitivity to post-fire management practices create conservation challenges, and black-backed woodpeckers are frequently monitored as a management indicator species in mixed-conifer forests of the western U.S. (Siegel et al., 2018).

My dissertation research addresses fundamental questions about the ways that animals respond to fire characteristics and persist in fire-prone landscapes using the black-backed woodpecker as a model post-fire specialist. My research seeks to investigate two broad questions: How do animals use and react to the temporary resource pulses created by fire? How do animals respond to variation in fire characteristics? I examine these questions using a variety of approaches that incorporate advances in molecular techniques, detailed field observations, broad population monitoring, and ecological modeling.

In Chapter 1, I examine how environmental factors associated with burned habitat, as well as temporal variables, affect black-backed woodpecker nest site selection and nest survival in northern California. I present evidence for strong relationships between black-backed woodpecker nest site selection and fire characteristics. Temporal factors, rather than habitat, showed effects on nest survival within burned areas, demonstrating a pattern of neutral congruence between habitat selection and a measure of fitness. Black-backed woodpeckers placed their nests in areas burned at high severity, but also selected nest sites near ecotones between high- and low-severity patches. This result provides added nuance to the habitat associations of this species, and I examine the potential hypotheses underlying this relationship as groundwork for future research.

In Chapter 2, I test the hypothesis that pyrodiversity may benefit individual species through habitat complementation, where multiple fire characteristics are needed for an individual to meet resource requirements at different life stages (Kelly et al., 2017). Using data from a multiyear radio-telemetry study in northern California, I show evidence for age-specific habitat relationships in black-backed woodpeckers and find that both adults and fledglings select habitat with greater variation in burn severity. I propose a novel mechanism driving the

pyrodiversity–biodiversity hypothesis centered on the potential for individual species to benefit from pyrodiversity in light of the predation-starvation hypothesis (Houston et al., 1993), which posits a trade-off between foraging efficiency and the need to minimize predation risk.

In Chapter 3, I empirically test the prediction that black-backed woodpecker juvenile survival responds to variation in fire characteristics. This prediction stems from the hypothesis that black-backed woodpeckers exhibit age-specific habitat relationships due to the tradeoff between high-quality foraging and predation risk in high-severity patches. Although high-severity fire provides foraging and nesting sites that support the needs of adult black-backed woodpeckers, I show that fledgling survival is greater in areas burned at lower severity. I suggest that pyrodiversity may enhance the survival and persistence of fire-associated animals by linking breeding and foraging habitat with neighboring areas of reduced predation risk.

In Chapter 4, I examine how black-backed woodpeckers combat the challenge of tracking the unpredictable rise and fall of post-fire resources across space and time. Theory predicts that resource pulse specialists like the black-backed woodpecker should use conditional dispersal strategies that allow them to emigrate from declining resource pulses and colonize new ones as they appear. Here, I present evidence that natal dispersal may act as a mechanism driving the pattern of woodpecker colonization and gradual population decline over the decade following forest fire.

In Chapter 5, I use a molecular approach to ask how four different woodpecker species use the arthropod food resources available in fire-prone landscapes. I characterize the diets black-backed woodpeckers, northern flickers (*Colaptes auratus*), white-headed woodpeckers (*Dryobates albolarvatus*), and hairy woodpeckers (*D. villosus*), primarily using fecal and cloacal swab samples collecting from nestlings in burned areas. Woodpeckers are

frequently used as indicators to evaluate forest management activities, and this detailed analysis of woodpecker diet using high-throughput sequencing represents an important step in understanding their resource requirements in disturbance-prone forests.

Globally, emerging evidence has demonstrated shifts toward fire regimes with higher burn severity and larger fire size, leading to increased focus on fire-associated species and the lessons they teach us about the historic role of fire (Kelly et al., 2020; Stephens et al., 2019; Westerling et al., 2006). In addition, post-fire systems are gaining more recognition for their unique ecological value and contribution to patterns of biodiversity across landscapes (He et al., 2019; Hutto et al., 2016). This dissertation advances our knowledge by using a model post-fire specialist to show how fire-associated species can respond to fire characteristics through resource selection, survival, and dispersal. These findings highlight the importance of pyrodiversity for animals that use post-fire habitat and demonstrate how fire-associated species can locate and track patchy, ephemeral resources after fire. Last, this work offers important insights into the complex and nuanced relationship between biodiversity and fire at a time when land managers face an emerging set of challenges in fire-prone landscapes.

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Chapter 1:
Nest site selection and nest survival of Black-backed Woodpeckers
after wildfire

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ABSTRACT

Recently burned coniferous forests host wildlife communities that respond to variation in burn severity, post-fire habitat structure, and patch configuration. Habitat selection theory predicts that birds inhabiting these variable post-fire landscapes will select nesting locations that confer an adaptive advantage through increased fitness and reproductive success. Understanding the effect of post-fire habitat on avian nesting ecology can provide valuable information to guide restoration and management after wildfire. The Black-backed Woodpecker (*Picoides arcticus*) is strongly associated with recently burned forests in the western U.S., where it is used as an indicator species for the effects of post-fire forest management. Between 2011 and 2018, we located and monitored 118 Black-backed Woodpecker nests in burned forests of northern California. We evaluated the influence of habitat and nest characteristics on nest site selection and daily nest survival. Our results demonstrate a pattern of neutral congruence between habitat selection and fitness. Black-backed Woodpeckers showed strong selection for each of the nest habitat variables that we measured: woodpeckers selected moderately-sized trees in areas of high snag density burned at high severity, but also in areas relatively close to low severity or unburned edges. However, only nest initiation date affected nest survival, with decreased survival in late-season nests. Our results suggest that management actions aimed at maintaining breeding habitat for Black-backed Woodpeckers should prioritize retention and creation of pyrodiverse landscapes that include dense stands of snags (>5 snags/100 m²) within ~500 m of forest that burned at low severity or remained unburned.

INTRODUCTION

Before raising young, birds must make a series of decisions at a variety of spatial scales regarding the location of breeding activities (Hildén, 1965; Johnson, 1980). These behavioral choices often result in fitness consequences manifested through nest success, such that selected habitats yield increased fitness (Chalfoun & Schmidt, 2012; Hildén, 1965; Martin, 1998). However, empirical studies of nesting ecology do not always demonstrate positive relationships, or congruence, between the factors important for nest site selection and the factors that affect fitness (Chalfoun & Schmidt, 2012). For example, incongruent relationships between habitat selection and fitness may arise if settlement cues become decoupled from their historic outcomes, as in ecological traps (Schlaepfer et al., 2002). In a review of studies on avian nesting ecology, Chalfoun and Schmidt (2012) found that over 50% of studies reported some form of neutral congruence, where habitat had an effect on nest site selection without showing a detectible effect on reproductive success.

The high prevalence of neutral congruence in avian breeding biology underscores the importance of considering the relationship between nest site selection and nest success (the probability that at least one nestling fledges) when evaluating management actions that affect bird populations. Effective management will both promote suitable breeding habitat to increase breeding bird abundance and promote the habitat characteristics within selected habitats that increase the probability of nest success (Chalfoun & Martin, 2007). Studies that link nest site selection and nest success may also reveal separate effects of habitat – if habitat influences one process but not the other, managers can leverage this information to guide where and how to efficiently invest management resources. This may prove especially valuable in management of

burned forests, where management decisions are often time sensitive and may have significant impacts on post-fire bird communities (Hanson & North, 2008; Noss et al., 2006).

The Black-backed Woodpecker (*Picoides arcticus*) is a habitat specialist strongly associated with high densities of standing dead trees (snags) used for foraging and nesting substrates (Hutto, 2008; Nappi & Drapeau, 2009; Tremblay et al., 2016). Throughout their range in the montane western U.S., Black-backed Woodpeckers are predominantly found within recently burned forests, where they forage primarily on the larvae of woodboring beetles that rapidly colonize dead and dying trees after wildfire (Murphy & Lehnhausen, 1998). Previous research in the western U.S. has demonstrated selection for territories and nest sites in areas with high snag densities created by severe wildfire (Seavy et al., 2012; Tingley et al., 2014), although the species is also found in lower densities in unburned forest (Fogg et al., 2014). Black-backed Woodpecker abundance generally peaks within 5 years after fire, followed by sharp declines as snags deteriorate (Tingley et al., 2018).

Given the specialized habitat preferences of Black-backed Woodpeckers, habitat selection theory predicts that individuals should select nest locations based on habitat conditions that correlate with increased nest success. Dense snag stands that burned at high severity likely provide increased access to food resources for Black-backed Woodpeckers (Murphy & Lehnhausen, 1998; Nappi et al., 2003), and nest success may be higher for nests near foraging habitat. Nest success also may reflect proximity to edge habitats; nests of other woodpecker species located nearer to habitat edges (i.e., ecotones between high and low severity burn patches) have shown lower daily survival rates due to higher predation rates (Fisher & Wiebe, 2006; Saab et al., 2011). At a finer scale, nest success may respond to microhabitat

characteristics such as tree diameter (Wiebe, 2001), nest cavity orientation (Hooge et al., 1999), and nest height (Fisher & Wiebe, 2006), which influence nest temperature and predation risk.

When neutral congruence exists between the habitat characteristics that affect nest site selection and nest success, we might expect daily nest survival to be primarily driven by a variety of abiotic/temporal variables. For example, nest initiation date may relate to breeding success because of resource matching, temporal trends in female quality, or seasonal temperature increases (Perrins, 1970; Socolar et al., 2017; Verhulst & Nilsson, 2008). Regional temperature extremes have also been correlated both positively and negatively to daily nest survival in cavity nesting species (Newlon & Saab, 2011; Saab et al., 2011; Socolar et al., 2017). In burned forests, daily nest survival rates may decrease with increasing years since fire due to increases in nest predator populations, decreases in available snags, or decreases in prey density within snags that persist (Rota et al., 2014). While land managers generally cannot control abiotic/temporal variables, understanding how these factors relate to nest success can be important in making management decisions.

Burned forests are often targeted for snag removal to serve a variety of objectives, including hazard tree removal, economic gain, re-planting, and reducing the risk of subsequent fire. These management actions have the potential to reduce populations of fire-associated species like the Black-backed Woodpecker (Hanson & North, 2008; Tarbill et al., 2018), leading to conflict between management objectives after fire. Information on the factors that influence nest site selection and nest success, as well as descriptive information on the timing of breeding activities, can help managers reduce conflicts between wildlife-related objectives and other management needs.

In this study, we examined the effect of variation in post-fire habitat characteristics on Black-backed Woodpecker nesting ecology in California. Specifically, our objectives were to (1) identify important habitat components in burned forests that increase the probability of Black-backed Woodpecker nest site selection, and (2) evaluate the influence of habitat characteristics, nest characteristics, and abiotic/temporal factors (i.e., temperature, nest initiation date, day of nesting period) on Black-backed Woodpecker nest success. We predicted that the biotic factors with a strong influence on nest site selection would show adaptive significance by also affecting daily nest survival, as expected under the theory of adaptive habitat selection (Hildén, 1965; Martin, 1998). Alternatively, we evaluated the prediction that there would be a lack of congruence between the factors that influence nest site selection and nest success in post-fire forests. We sought to provide information to help guide conservation of Black-backed Woodpeckers in the context of post-fire forest management.

METHODS

Study sites

We studied Black-backed Woodpecker nest sites within the perimeters of 6 wildfires that burned in Plumas and Lassen National Forests, California (Figure 1). The Peterson (burned in 2008) and Bald (2014) fires burned predominately eastside pine forest comprised of *Pinus ponderosa*, *P. jeffreyi*, *Calocedrus decurrens*, and *Juniperus occidentalis*. The Moonlight (burned in 2007), Wheeler (2007), Sugarloaf (2009), and Chips (2012) fires burned primarily Sierran mixed conifer forest dominated by *P. ponderosa*, *Abies concolor*, *A. magnifica*, *Pseudotsuga menziesii*, and *C. decurrens* (Supplemental Material Table S1). Study areas ranged

from ~1,100–2,100 m elevation and spanned 2–10 years post-fire at the time of data collection. We collected data at some fires in up to 4 consecutive years (Supplemental Material Table S2).

Nest searching and monitoring

We searched for woodpecker nests from mid-April to late July, 2011–2018, using broadcast surveys to detect territorial individuals. Rather than systematically searching a small portion of each fire, we attempted to saturate as large an area as logistically feasible through exploratory searching, although we were unable to cover the full extent of each fire due to their large sizes (up to 30,897 ha) and limited road access. Surveyors broadcast Black-backed Woodpecker vocalizations and territorial drumming obtained from The Macaulay Library of Natural Sounds (Cornell Laboratory of Ornithology; recorded by G.A. Keller). Once detected, we attempted to follow individuals back to their nest site and used behavioral cues to locate the nest cavity. We also captured and radio-tagged a subset of adult Black-backed Woodpeckers ($n = 49$) as part of a separate study of home range size and habitat selection (Stillman et al., 2019a; Tingley et al., 2014), and we supplemented our nest searching by following tagged individuals to their nests. Radio-tagged individuals did not perceptibly alter their behavior around nests, and we found no evidence that radio-tags influenced adult or nest survival (apparent nest success rate was 0.82 and 0.71 for tagged and untagged birds, respectively). Additional information on capture and tagging methods can be found in Tingley et al. (2014).

We visited nests every 2–5 days (mean interval = 3.5 days) to record nest status and activity until fledging or failure. We assigned nest stage at each visit (laying, incubating, nestling) using adult and nestling behavioral cues during 15–60-minute observation periods. We recorded nests as successful if they appeared to be empty on or near the expected fledging day and if nestling behavior during the previous visit suggested that nestlings would fledge soon

(e.g., mature vocalizations, poking head out of cavity, advanced feather development, etc.). In many cases (59 out of 118 nests), we were able to confirm nest success with observations of recent fledglings in the vicinity. We recorded nest failure if the nest appeared empty or occupied by a different species well before the expected fledge date, or if there were clear signs of depredation (e.g., eggs crushed inside cavity, gnaw marks at cavity entrance). If we were unable to confidently assign nest fate (10 out of 118 nests), we excluded the last observation interval from our nest survival analysis.

Habitat predictors of nest site selection and survival

We examined multiple nest, habitat, and abiotic/temporal variables (Table 1). Tree diameter and nest cavity orientation may regulate cavity temperature profiles with potential effects on survival (Hooge et al., 1999; Wiebe, 2001), and nests that are higher may provide greater protection from ground-based predators (Fisher & Wiebe, 2006). At a broader scale, we predicted that woodpeckers would place nests in pyrodiverse areas near the edges of high severity patches in order to maintain proximity to preferred high-cover habitat for young fledglings while maintaining access to snag-dense foraging sites (Stillman et al., 2019a). Alternatively, we also evaluated whether nests near habitat edges (i.e., between high and low severity patches) would experience higher predation rates (Fisher & Wiebe, 2006; Saab et al., 2011).

After nests fledged young or failed, we measured characteristics of nest trees and the habitat around each nest (Table 1). At the nest tree, we recorded four variables: diameter at breast height (DBH), cavity orientation, cavity height, and tree height. For habitat characteristics surrounding the nest, we counted the number of snags with DBH > 10 cm within a 10-m radius and collected 2 additional variables using remote sensing data. First, we used 30-m resolution

Landsat-derived GIS data from the Rapid Assessment of Vegetation Condition after Wildfire program (<https://fsapps.nwcg.gov/ravg/>) to extract the mean burn severity within 100 m of each nest tree, measured as the percent change in canopy cover from pre-fire to immediately after fire. Second, we measured the distance between the nest tree and the nearest forest patch burned at low severity or left unburned. We defined the threshold for “low severity” at $\leq 4.4\%$ change in canopy cover, which is the median raster value of points classified as low severity from a field survey of ~10,000 points within the study area (Stillman et al., 2018). Nests located within a stand that burned at low severity ($n = 4$) were assigned a distance of zero.

Abiotic/temporal predictors of daily nest survival

In addition to characteristics of nests and surrounding habitat, we also measured climatic and temporal variables with hypothesized ties to daily nest survival rate (Table 1). Given that our study sites were composed of open, snag-dominated habitats near the southern end of the species’ range, we predicted that high temperature anomalies at the regional scale would have a negative effect on woodpecker nest success (Saab et al., 2011; Socolar et al., 2017). We also predicted that nest success would be lower in late-season nesting attempts and that predation would be more likely when nests contained older, more vocal young (Kozma & Kroll, 2012; Verhulst & Nilsson, 2008).

We extracted daily maximum temperatures during the full 40-day period for each nest, regardless of nest fate, from the closest National Oceanic and Atmospheric Administration (NOAA) station to each nest (mean distance from nest to monitor = 10.6 km; data available at <https://www.ncdc.noaa.gov>). To calculate the daily anomaly in maximum temperature, we subtracted the mean maximum temperature experienced over the 40-day period from each daily value (Socolar et al., 2017).

We assigned an initiation date to each nest by counting backwards from observed transitions in nesting stage (laying, incubation, nestlings, fledglings) using published estimates of nesting period length (Tremblay et al., 2016). We assumed a 40-day full nesting cycle with 2 days for laying, 13 days for incubation, and 25 days between hatching and fledging, which proved consistent with our field observations. For successful nests, we estimated fledge date as the median date between the last nestling observation and the first post-fledging observation, and we back-counted 40 days to assign the initiation date. For failed or uncertain nest fates, we back-counted from our most confident nest transition date based on behavioral observations recorded during nest visits. Once each nest was given an initiation date, we assigned each interval between visits an ordinal day in the nesting period, from 1–40, by taking the median day between consecutive visits.

Sample of available nesting locations

We evaluated nest site selection by comparing used nest locations to a sample of available nest locations at 2 spatial scales that are biologically relevant in our study system (Jones, 2001). First, we evaluated nest stand selection at the home range scale by randomly selecting 5 “available” nest locations from an 806-m radius buffer around each nest. This buffer encompassed an area of 204 ha, which is the average minimum convex polygon home range size for Black-backed Woodpeckers in our study area (Tingley et al., 2014). This method allowed us to investigate third-order habitat selection – the selection of nest characteristics from within the individual’s home range (Johnson, 1980). For each available location, we extracted the mean burn severity and the distance between the available point and the nearest low severity or unburned edge, as above.

Second, we used field-based measurements to compare the used nest tree and available trees in a manner consistent with fourth-order habitat selection – the selection of specific resources from a resource patch (Johnson, 1980). As part of 2 separate studies (Stillman et al., 2019a; Tingley et al., 2014), we established systematic 200 x 200-m grids of sampling points covering the minimum convex polygon of tracking locations for individual radio-tagged birds in each of the 6 fires. We used the subset of nests that overlapped the boundaries of sampling grids ($n = 53$) in our analysis of nest tree selection, and we generated an available sample by selecting the 5 closest grid points to each nest in the subset (mean distance = 137 ± 88 m SD). At each grid point, we measured the DBH of the closest snag and counted the number of snags with DBH > 10 cm within a 10-m radius of the point. We selected only snags (rather than live trees) for the available sample because the vast majority (98%) of our nests occurred in snags.

Nest site selection analysis

We examined the biotic factors that influence nest site selection in 3 steps representing 3 spatial scales: (1) nest stand selection, (2) nest tree selection, and (3) nest cavity placement.

Nest stand selection. We used the full sample of nests to estimate relationships between nest stand selection and 2 GIS-derived landscape-level variables: burn severity and distance to low severity or unburned edge. We used a generalized linear mixed effects model to estimate the parameters of the exponential resource selection function in a Bayesian framework. Our model included a random fire-level intercept term to account for potential non-independence of nests within each fire (Gillies et al., 2006).

Nest tree selection. We used the subset of 53 nests that overlapped the systematic sampling grid to estimate relationships between nest tree selection and 2 field-measured variables: nest tree DBH and snag density around nest trees. We used a Bayesian generalized

linear mixed effects model with a random intercept term to account for multiple samples in each fire-by-year combination. We included a quadratic term for DBH based on expectations from our field observations and Seavy et al. (2012).

Both nest selection models (stand and tree) contained 5 available locations for every nest location. We used vague normal prior distributions ($\mu = 0$, $\tau = 0.1$) on the intercept parameter and fixed effects, and a uniform (0.1, 3) prior distribution for the random effect standard deviation. We included initial values for all parameters based on a preliminary run of 1,200 iterations.

Nest cavity placement. We separately examined selection for 2 components of nest cavity placement: cavity orientation and cavity height above the ground. We tested for nonrandom cavity orientation using angular statistics and a Rayleigh test (Batschelet, 1981). Given a sample of directional orientations, this test measures the amount of dispersion around the mean vector and uses the relative index (r) to test the null hypothesis that the orientations are randomly distributed. An r value of 1.0 indicates that all points have the same orientation and a value of 0 indicates random orientation. We tested for selection in nest cavity height using a bootstrapping approach with paired t-tests to compare observed heights to a series of “available” nest heights. We generated the available distribution by iteratively sampling 1000 potential heights for each tree ranging from ground level to the measured tree height (for broken-top snags) or to 3 m below the measured tree height (for trees with intact tops). We used this method to avoid including portions of the tree trunk that were too thin to hold a potential cavity. For each of the 1000 samples, we used a paired t-test to calculate the average difference between observed and random nest placements and made inference on the 95% confidence interval of this test statistic.

Nest survival models

We modeled Black-backed Woodpecker daily nest survival (the probability that a given nest survives from day_x to day_{x+1}) using logistic exposure models fit within a Bayesian framework (Schmidt et al., 2010). These models support the inclusion of fixed and random effects in a hierarchical structure that accounts for the inherent multilevel design of nest survival studies (i.e., multiple observations per nest). In addition, our models allow for uneven sampling intervals and inclusion of interval-specific covariates.

The survival of nest i over observation interval j was assumed to follow a Bernoulli distribution $y_{i,j} = \text{Bernoulli}(\theta_{i,j})$ where $y_{i,j} = 1$ if nest i survived interval j , $y_{i,j} = 0$ if the nest failed, and $\theta_{i,j}$ is the probability of nest i surviving interval j . Here, θ represents the daily survival probability, s , raised to the length of the risk exposure period such that $\theta_{i,j} = s^{t_{i,j}}$, where $t_{i,j}$ is the length of interval j for nest i . We modeled the logit-transformed daily nest survival probability as a function of nest-level and interval-level covariates. We included a nest-level identifier as a random intercept in each model to account for multiple observations of each nest over the breeding period.

Model selection. We developed a set of 14 nest survival models based on *a priori* hypotheses for our system and purposefully sought to test all variables included in our nest site selection analysis. We considered 10 potential covariates comprising 3 categories: nest characteristics, habitat characteristics, and abiotic/temporal variables (Table 1). Rather than evaluate every possible combination of covariates, we built models with covariate combinations meant to test specific hypotheses about our system based on previous research (Forristal, 2009; Kozma & Kroll, 2012; Saab et al., 2011) (Table 2, Supplemental Material Table S3).

We compared the 14 fitted Bayesian models of nest survival using leave-one-out cross-validation to estimate the pointwise out-of-sample prediction accuracy (Vehtari et al., 2017). We

employed an efficient computation of cross-validation that uses Pareto-smoothed importance sampling, implemented through the R package “loo” (Vehtari et al., 2018). The top-performing model was then selected using the difference in leave-one-out information criteria (LOOIC); this value is presented on the deviance scale, similar to other information criterion approaches. To corroborate our model selection results, we also calculated the widely applicable information criterion (WAIC; Watanabe, 2010), a generalization of the Akaike information criterion, and confirmed that both model selection approaches selected the same top model (see Supplemental Material Table S3 for WAIC-based results).

For all nest survival models, we included an informed prior on the global intercept based on a previous study in burned mixed-conifer forest, which estimated the daily survival rate for Black-backed Woodpecker nests at 0.994 ± 0.2006 SE (Forristal, 2009), giving a logit-scale prior distribution as *Normal*($\mu = 5.109978$, $\tau = 0.086$). We used vague normal prior distributions ($\mu = 0$, $\tau = 0.1$) on all fixed effects and a uniform prior (0.1, 3) on the random effect. Data exploration indicated linear relationships with DBH and nest day, so we included both variables as linear terms rather than as quadratic predictors. We included time since fire in our group of habitat characteristics due to its notable effects on habitat structure (Smucker et al., 2005).

Bayesian inference

We fit all Bayesian models using JAGS and the package “R2jags” in R (R Core Team, 2020; Su & Yajima, 2015). Models ran 3 chains of 20,000 iterations thinned by 10 with a burn-in of 5,000, yielding a final posterior sample of 4,500. We visually inspected traceplots to assess chain convergence and confirmed that the Gelman-Rubin statistic was <1.1 for every parameter estimate (Gelman et al., 2004). We centered and standardized continuous variables prior to modeling, and we present inference on parameters using 95% Bayesian credible intervals. The

predictor variable for cavity orientation was centered by calculating the absolute value circular distance from the mean angle, so that orientations that deviate further from the mean had larger values.

To evaluate fit for the nest selection models, we created a test statistic based on the observed and predicted ratio of used to available points and conducted posterior predictive tests with associated Bayesian p-values (Gelman et al., 1996). Similarly, we conducted a posterior predictive check for the top nest survival model by calculating the Bayesian p-value for a test statistic based on the observed/predicted ratio of interval-level nest failures and nest successes. We considered Bayesian p-values less than 0.1 or greater than 0.9 as evidence for lack of fit (Gelman et al., 1996).

RESULTS

We located 118 Black-backed Woodpecker nests within the boundaries of the 6 wildfires and monitored nests for a total of 956 observation intervals (mean = 8 visits to each nest).

Nest site selection

The average burn severity, measured as % change in canopy cover within 100 m of nests, was $82 \pm 2\%$ SE, and the average distance between nests and the closest low severity or unburned edge was 255 ± 21 m. Woodpeckers nested at sites with a mean of 15 ± 1 snags within 10 m of the nest tree (95% quantile = 2–31 snags), and the average nest tree had a DBH of 37 ± 1 cm (95% quantile = 22–67 cm). All but 2 nests (98%) occurred in dead trees.

Resource selection models showed significant positive selection for habitat patches that burned at high severity (Table 3, Figure 2A). For example, a high severity burn patch with 100% change in canopy cover (i.e., all trees killed) was over 5 times more likely to be used as a nest

site than a patch with 50% canopy cover change. However, woodpeckers also selected sites that were relatively close to low severity or unburned edges, showing greater probability of nesting near high–low severity ecotones than in the center of large high severity patches (Table 3, Figure 2B).

We used data from a subset of 53 nests with field-based systematic habitat sampling to estimate the effect of tree diameter and snag density on nest tree selection. Woodpeckers showed a strong quadratic relationship to tree DBH, with peak probability of use at 47 cm (Table 3, Figure 2C). As snag density increased, the relative probability of nest tree use also increased (Figure 2D). Nest sites with 15 snags within a 10-m radius (equal to a density of ~5 snags per 100 m²) had a 50% relative probability of use.

Nest cavities showed a strong bias in orientation, with nonrandom clustering around the circular mean orientation of 80.6° (Rayleigh $r = 0.36$, $p < 0.001$) (Figure 3A). The average nest cavity height was 4.8 ± 0.4 m (Figure 3B), which was significantly lower by 1.2 m (95% CI: -1.9, -0.5) than would be expected if nest height was uniformly random.

Nest survival

We observed nest failure at 27 of 108 nests with known fates, yielding an apparent nest success rate of 0.75. Though we were not able to confidently determine the cause of failure for most nests, we documented probable occurrences of nest predation by small mammals, two occasions of nest predation by American black bears (*Ursus americanus*), and one occasion of nest eviction by European Starlings (*Sturnus vulgaris*). We recorded failures for 3 nests during the laying stage, 12 during incubation, and 12 during the nestling stage. The median nest initiation date was May 3, and 75% of nests were initiated between April 21 and May 20 (Figure

4A). For documented successful nests ($n = 81$), the median fledge date was June 8 and 75% of successful nests fledged between May 30 and June 23 (Supplemental Material Figure S1).

We evaluated 14 Bayesian nest survival models with 10 potential covariates. The top model for nest survival included initiation date and nest day (Table 2), but only initiation date showed a strong effect on nest survival (Table 3, Figure 4). Models which fit better than the intercept-only model included abiotic variables alone (Table 2), without any factors related to habitat or nest characteristics. Model estimates indicated that woodpecker nests which began later in the breeding season had a lower probability of survival, with daily survival rate dropping precipitously for nests initiated after May 20 (Figure 4B). Under average conditions, the top model estimated baseline daily survival rate at 0.996 (95% CI: 0.991, 0.999) and overall nest success rate at 0.852 (95% CI: 0.697, 0.961).

Model fit

Both nest selection models closely approximated a test statistic derived from the expected number of used versus available locations (Supplemental Material Figure S2). Bayesian p-values indicated no significant lack of fit, with $p = 0.49$ for the model of nest stand characteristics and $p = 0.48$ for the model of tree characteristics. Similarly, our posterior predictive test on the expected ratio of nest successes versus failures found no evidence for lack of fit in the top nest survival model (Bayesian $p = 0.48$).

DISCUSSION

In our study, Black-backed Woodpeckers showed strong habitat selection at the scale of nest stand, nest tree, and nest placement by narrowly choosing nesting locations relative to available habitat. However, variation in these selected habitat conditions across monitored nests

showed no evidence for an effect on nest survival; rather, abiotic/temporal variables alone, and nest initiation date in particular, provided the best predictors of nest survival. Consequently, Black-backed Woodpecker nesting ecology in burned forests of northern California demonstrated a pattern of neutral congruence between the habitat characteristics important to nest site selection and nest survival.

Although theory predicts that nest site selection should show adaptive significance, our observational study did not detect a significant effect of habitat on nest survival. It is plausible that the main selective pressures operating in our study system (i.e., predation risk) were random or unpredictable within the range of selected habitats. This explanation is consistent with the adaptive peaks hypothesis (Latif et al., 2012; Wright, 1932), which suggests that some bird populations may only nest in habitat that is already “adaptive,” and thus may not express sufficient variation in habitat selection necessary to detect links between fitness and habitat. Alternatively, nest site selection may respond primarily to other fitness components that were not part of our study, such as adult condition, adult survival, clutch size, or fledgling survival. Some aspects of nest site selection may also respond primarily to availability rather than apparent fitness benefits. For example, Black-backed Woodpeckers may select specific nest cavity locations based solely on the availability of suitable excavation sites on the nest tree instead of perceived predation risk (Lorenz et al., 2015).

Black-backed Woodpeckers are known to occur in low densities in unburned forests throughout the species’ range (Fogg et al., 2014; Tremblay et al., 2015a), but our study focused entirely on birds detected inside the perimeters of recent fires. Previous research elsewhere in the species’ range suggests that reproductive success is lower outside of wildfire perimeters (Rota et al., 2014), and populations within recently burned forest may act as source populations for the

surrounding region (Nappi & Drapeau, 2009). Future work directly comparing reproductive success in burned versus unburned habitats would be beneficial (Tremblay et al., 2015a).

Post-fire logging has been demonstrated to reduce Black-backed Woodpecker abundance, likely by reducing the amount of available habitat for nesting and foraging (Hanson & North, 2008; Saab et al., 2007). Post-fire logging treatments at the fires that we sampled included a broad spectrum of actions, ranging from limited roadside hazard tree removal to stand harvest for biofuel. While we attempted to prioritize nest searching in intact stands, our sample included some nests near previously logged areas. One nest was located in an area of active logging, and management personnel retained a small cluster of trees around the nest, which fledged successfully, although both fledglings from this nest were predated soon after fledging (Andrew Stillman, unpublished data). While we did not test effects of post-fire logging on nest site selection or survival, the presence of these operations could have decreased the density of breeding Black-backed Woodpeckers in some study areas and may have caused some birds to select habitat outside of affected stands.

Nest site selection

Woodpeckers tended to select nest locations in high burn severity patches (Figure 2A), but typically within 500 m of low severity patches or unburned edge (Figure 2B). Recently fledged Black-backed Woodpeckers generally move out of high-severity burn stands to seek greater cover (Stillman et al., 2019a), and we speculate that selection for nest sites closer to edges of high severity patches provides easier access to preferred fledgling habitat, which may increase fledgling survival. Furthermore, proximity to fire edges or low-severity patches may have direct consequences on nest success, although we did not detect these effects in our study. In Quebec, Black-backed Woodpecker nests in burned forests showed increased productivity

closer to unburned edges (Nappi & Drapeau, 2009), perhaps due to increased concentrations of *Monochamus scutellatus* woodboring beetle larvae in these areas (Saint-Germain et al., 2004). However, in Idaho, Saab et al. (2011) found that nest success decreased closer to unburned edges, perhaps because unburned forests act as a source for nest predators. Apparent differences in the effect of distance to edge on Black-backed Woodpecker nesting ecology may stem from regional differences in predator communities, forest types, or fire severity patterns. While we did not detect any relationship between nest survival and distance to edge at our study sites in northern California, we note that our woodpeckers nested farther from the edge on average than nests recorded by Saab et al. (2011) (mean distance to unburned or low severity edge in California = 255 m, mean distance to unburned edge in Idaho = 159 m).

Although Black-backed Woodpeckers are known to preferentially forage on larger-diameter trees (Nappi et al., 2003), the birds in our study selected moderate-sized trees for nests, consistent with previous research in northern California (Seavy et al., 2012). Smaller-diameter trees (i.e., < 15 cm DBH) are likely too thin to allow for cavity excavation, and larger-diameter trees may have comparatively reduced internal wood softening from wood-rotting fungi. When selecting excavation sites, Black-backed Woodpeckers may respond primarily to wood hardness rather than external tree characteristics (Lorenz et al., 2015). Given this, it is reasonable to expect regional discrepancies in favored nest tree characteristics due to geographic variation in fungal communities as well as the species and size of available trees. For example, Black-backed Woodpeckers in South Dakota selected relatively smaller nest trees with an average DBH of 25 cm (Bonnot et al., 2009), whereas birds in our northern California sites selected moderate-sized trees with an average DBH of 37 cm.

Nest cavities were lower than expected by chance, despite potential threats from ground-based predators. In addition to probable nest predation from small mammals, we documented 2 occurrences of nest predation by American black bears, which climbed trees to forcibly chew and claw a large opening at the cavity entrance. Although we did not detect an effect of nest height on survival, we hypothesize that higher nests may incur additional risks that balance nest placement towards the moderately low heights that we observed, such as an increased risk of snags snapping and falling at a point below the cavity.

Nest survival in selected habitats

Despite the strong effect of habitat on nest selection, nest initiation date was the only significant predictor of daily nest survival probability. Reproductive success declines over the course of the breeding season for many bird species, although the direct mechanisms leading to this phenomenon are often complex (Kozma & Kroll, 2012; Verhulst & Nilsson, 2008). These seasonal patterns may stem either from variation in environmental quality (e.g., food availability, temperature extremes, predator abundance) or seasonal trends in the quality of breeding individuals (e.g., high quality females breed first) (Perrins, 1970). In our study system, we propose two potential mechanisms for the initiation–survival relationship. First, increased failure in later nests may result from breeding attempts by lower-quality individuals that renested after initial nest failures. Black-backed Woodpeckers generally raise one brood per breeding season, but they will excavate a second nest in a different tree if the first nest fails (Tremblay et al., 2016). We observed that 5 of 6 confirmed renesting attempts failed, and we suspect that some additional late nesting attempts in our sample came from renesting birds. Second, later nests may be exposed to increased risk of predation by nest predators that show temporal trends in nest predation rates (Fisher & Wiebe, 2006).

Although past studies have demonstrated an effect of temperature on woodpecker nest success (Newlon & Saab, 2011; Saab et al., 2011), temperature variation at the regional scale did not have a direct effect on daily nest survival in our study area. This result could arise from not directly measuring temperature at active nests, as cavity-nesting birds can potentially mitigate the effects of temperature extremes by selecting appropriate microhabitat characteristics. East-facing cavities, which represented the majority of our 118 nests, are thought to mediate temperature fluctuations in cavity-nesting species – nests that face east average higher morning temperatures and cooler afternoon temperatures than nests that face other directions (Hooge et al., 1999; Tremblay et al. 2015b).

Our results did not support our prediction that Black-backed Woodpecker nest success decreases with increasing time since fire. Although we sampled some fires in multiple consecutive years, we primarily employed a space-for-time substitution in order to build a sample of fires ranging from 2–10 years post-fire. Because fires differed in elevation, latitude, and forest composition, it is possible that environmental differences between study sites masked a true decline in survival with increasing time since fire. However, the strong relationship between habitat and nest site selection suggests that, even >7 years post-fire, woodpeckers may still maintain high quality nest sites by selecting for remaining stands of dense snags in high severity burn patches. Thus, the gradual decrease in snag density or prey abundance with time since fire may show a stronger effect on woodpecker abundance than on nest success. In this scenario, decreases in suitable habitat would cause a decrease in abundance even as nest success remains constant. Previous research has repeatedly demonstrated temporal declines in Black-backed Woodpecker occupancy, population persistence, and nest density with increasing time

since fire (Saab et al., 2007; Tingley et al., 2018; Matseur et al., 2019), with conflicting evidence for coincidental declines in nest survival (Nappi & Drapeau, 2009; Rota et al., 2014).

Management implications

Fire regimes in the American West are increasingly characterized by large, homogenously severe wildfires, prompting concern for the conservation of forest bird populations (Miller & Safford, 2012; Stevens et al., 2017; Tingley et al., 2016). It may seem that post-fire specialists like the Black-backed Woodpecker stand to benefit from an increased prevalence of high severity post-fire landscapes in California, but recent research suggests that this species seeks out more pyrodiverse areas – landscapes that have greater variation in burn severity – to meet the habitat preferences of both fledglings and adults (Stillman et al., 2019a). The finding that the woodpeckers in our study tended to select nest sites closer to the edges of high severity burn patches provides added evidence that pyrodiversity is an important component of Black-backed Woodpecker habitat within burned forests, consistent with research in other parts of the species' range (Nappi et al., 2010). We suggest that managers interested in providing nesting habitat for Black-backed Woodpeckers consider retention and creation of pyrodiverse landscapes that include dense stands of snags (>5 snags/100 m²) within ~500 m of stands that burned at low severity or remained unburned.

Managers may reduce conflicts between wildlife conservation and objectives that involve snag removal by altering the timing of habitat-altering activities. Our finding that nest success declines in later-season nests suggests that managers could reduce the immediate impact of logging activities on breeding Black-backed Woodpeckers by delaying actions until after most nests have fledged. At our study sites in northern California, 95% of nests had fledged by June

29, which may provide a useful benchmark for timing post-fire management that might disturb nesting habitat.

More generally, our results provide a caution for land managers interested in animal conservation: when a species exhibits strong behavioral selection for high quality habitat, purely observation studies may fail to reveal relationships between habitat and fitness (Chalfoun & Schmidt, 2012). In this scenario, abiotic/temporal variables – which are generally not controlled by land managers – will likely have the strongest effect on fitness components like nest success. We might expect this phenomenon to be especially prevalent in habitat specialists, where natural selection has presumably shaped behavioral habitat selection to reflect a narrow range of preferred conditions. When suitable habitat is abundant, habitat specialists can behaviorally select nest locations that confer a relative fitness advantage, and thus avoid the negative consequences of breeding in poor-quality areas.

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ETHICS STATEMENT

This research was conducted in compliance with the University of Connecticut Institutional Animal Care and Use Committee (IACUC protocol #A16-008), the California

Department of Fish and Wildlife (Scientific Collecting Permit #SC-8645), and the USFWS Bird Banding Laboratory (Permit #22423).

DATA DEPOSITS

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.n98q8s3> (Stillman et al., 2019b).

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Table 1. Covariates used in models of Black-backed Woodpecker daily nest survival. We grouped covariates into three categories while building the model set (nest characteristics, habitat characteristics, and abiotic/temporal factors) and explored different combinations of these covariate sets based on *a priori* hypotheses. We included nest characteristics and habitat characteristics in our analysis of nest site selection.

Covariate Set	Covariate name	Description
Nest Characteristics	Tree DBH	Tree diameter at 1.4 m (cm)
Nest Characteristics	Orientation	Orientation of the cavity entrance (°)
Nest Characteristics	Cavity height	Height from ground to the cavity entrance (m)
Habitat Characteristics	Distance to edge	Distance to the nearest low severity or unburned patch (m)
Habitat Characteristics	Burn Severity	The mean % change in canopy cover after fire, within 100 m
Habitat Characteristics	Snag count	Number of snags >10 cm DBH within 10 m
Habitat Characteristics	Time since fire	Number of years since the fire burned
Abiotic/temporal	Temp anomaly	Deviation from expected max temperature over the nesting period (°)
Abiotic/temporal	Initiation date	Julian day that the first egg was laid
Abiotic/temporal	Nest Day	Day of the nesting period, ranging from 1 to 40

Table 2. Model selection results for 14 candidate models of Black-backed Woodpecker daily nest survival. Bayesian model selection employed leave-one-out cross-validation to calculate the information criteria LOOIC, presented here on the deviance scale. Models are ranked by ascending LOOIC values, with Δ LOOIC given as the difference between each candidate model and the top-ranking model.

Model covariates	LOOIC	Δ LOOIC
Initiation date + Nest day	285.16	0.00
Initiation date + Nest day + Temp anomaly	288.11	2.95
Intercept only	288.69	3.53
Initiation date + Snag count + Burn severity + Distance to edge + Time since fire	293.32	8.16
Initiation date + Tree DBH + Cavity height + Orientation	294.20	9.04
Burn Severity + Time since fire	295.20	10.04
Tree DBH + Cavity height + Orientation	295.46	10.30
Cavity height + Distance to edge	296.98	11.82
Initiation date + Nest day + Temp anomaly + Snag count + Burn Severity + Distance to edge + Time since fire	300.14	14.98
Initiation date + Nest day + Temp anomaly + Tree DBH + Cavity height + Orientation	301.52	16.36
Cavity height + Distance to edge + Time since fire + Nest day	302.19	17.03
Snag count + Burn Severity + Distance to edge + Time since fire	304.28	19.12
Snag count + Burn Severity + Distance to edge + Time since fire + Tree DBH + Cavity height + Orientation	305.73	20.57
Initiation date + Nest day + Temp anomaly + Snag count + Burn Severity + Distance to edge + Time since fire + Tree DBH + Cavity height + Orientation	309.59	24.43

Table 3. Parameter estimates for models of woodpecker nest stand selection, nest tree selection, and daily nest survival. Nest selection models estimated the relative probability of resource use based on Bayesian generalized linear mixed-effects models. The nest survival model is the top Bayesian logistic exposure model from multi-model comparison (Table 2). Estimates show means and 95% Bayesian credible intervals.

Covariate	Parameter estimate
<i>Nest stand selection model</i>	
Intercept	-1.83 (-2.66, -0.86)
Burn Severity (% change in canopy cover)	1.76 (1.34, 2.18)
Distance to edge	-0.96 (-1.40, -0.57)
Standard deviation of random fire effect	0.94 (0.26, 2.29)
<i>Nest tree selection model</i>	
Intercept	-1.52 (-2.12, -0.97)
Snag count	1.36 (0.95, 1.78)
Tree DBH	2.20 (1.44, 3.08)
Tree DBH ²	-1.28 (-1.95, -0.75)
Standard deviation of random fire-year effect	0.41 (0.11, 1.13)
<i>Top nest survival model</i>	
Intercept	5.60 (4.70, 7.00)
Initiation date	-0.71 (-1.43, -0.17)
Nest day	-0.27 (-0.94, 0.26)
Standard deviation of random nest effect	1.43 (0.21, 2.86)

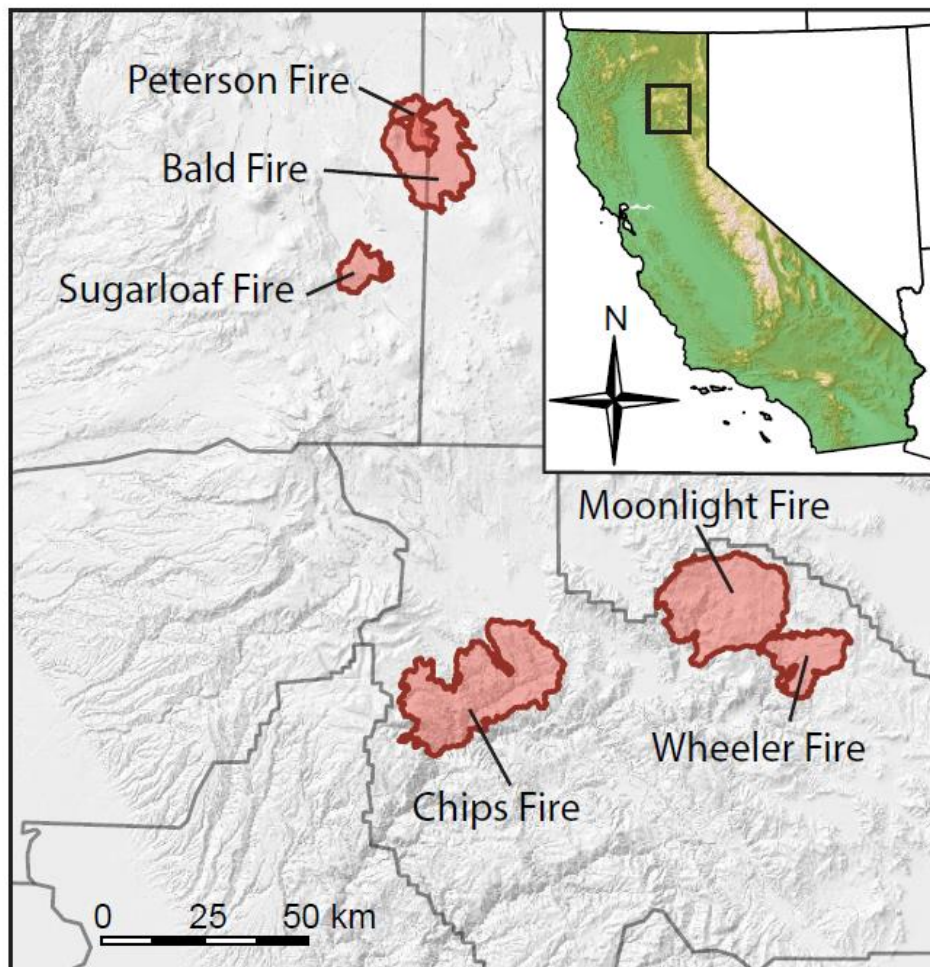


Figure 1. Locations of the six wildfires where Black-backed Woodpecker nests were monitored in northern California.

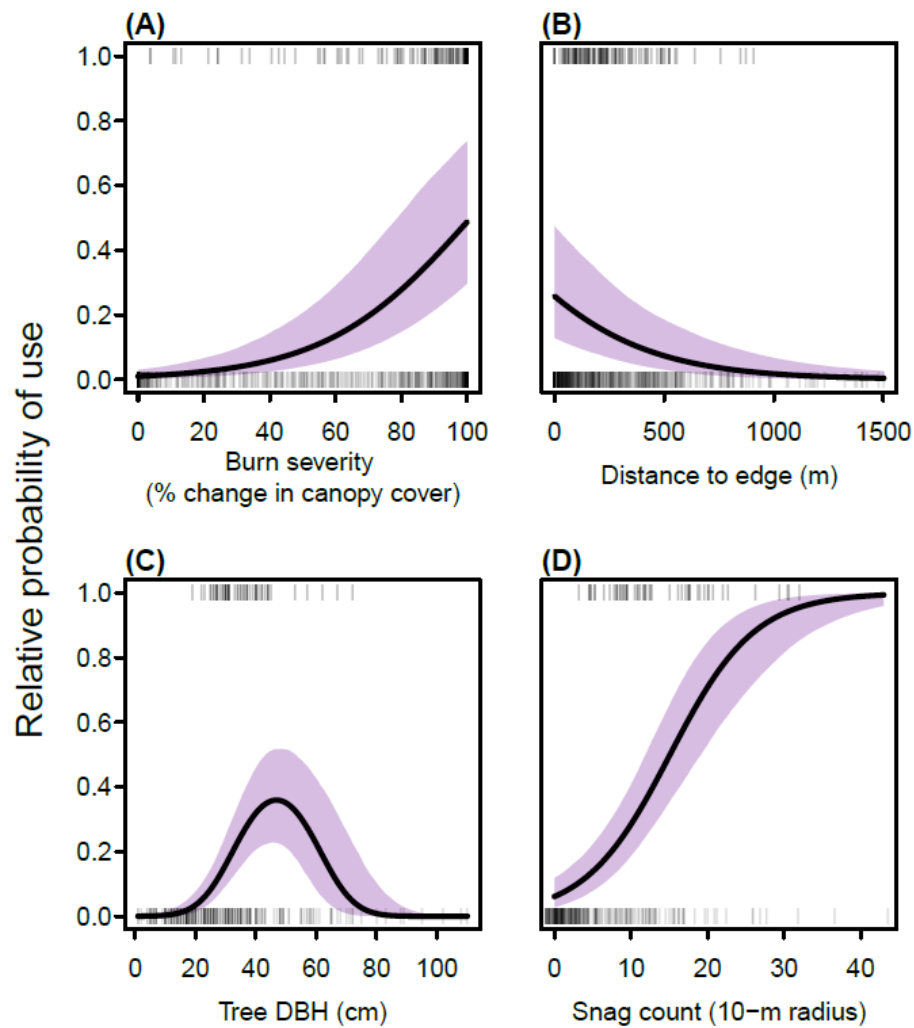


Figure 2. Modeled relationships for Black-backed Woodpecker nest stand selection (A, B) and nest tree selection (C, D). Thick black lines show the mean response predicted by the model, and shaded regions show 95% credible intervals. Rugs depict the raw data, with used nest locations drawn at $y = 1$ and available locations drawn at $y = 0$.

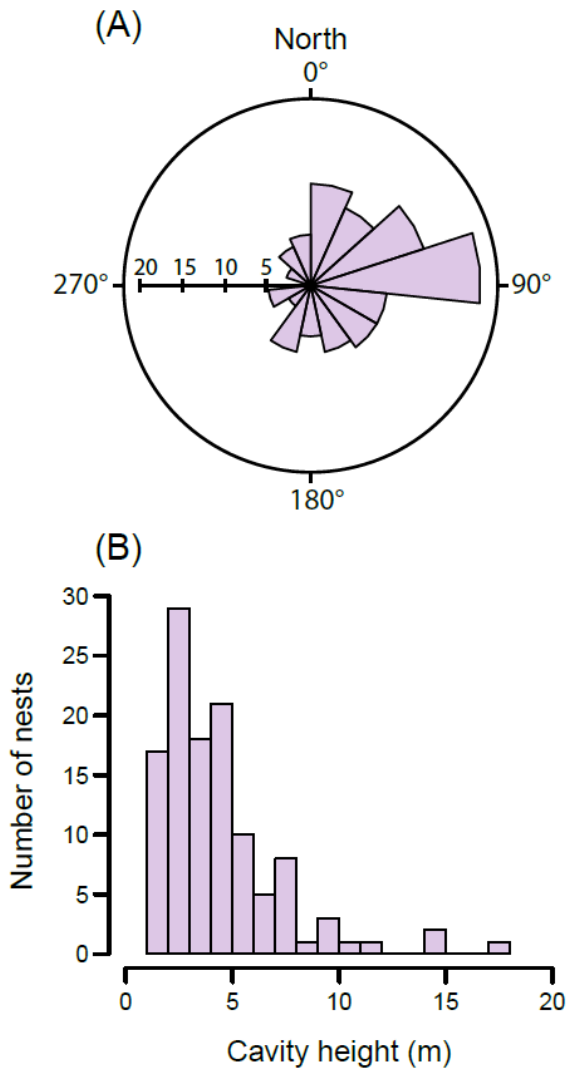


Figure 3. Nest cavity characteristics for 118 Black-backed Woodpecker nests in northern California, showing (A) the direction that nest cavities faced with sample size on the horizontal axis, and (B) a histogram of nest cavity heights.

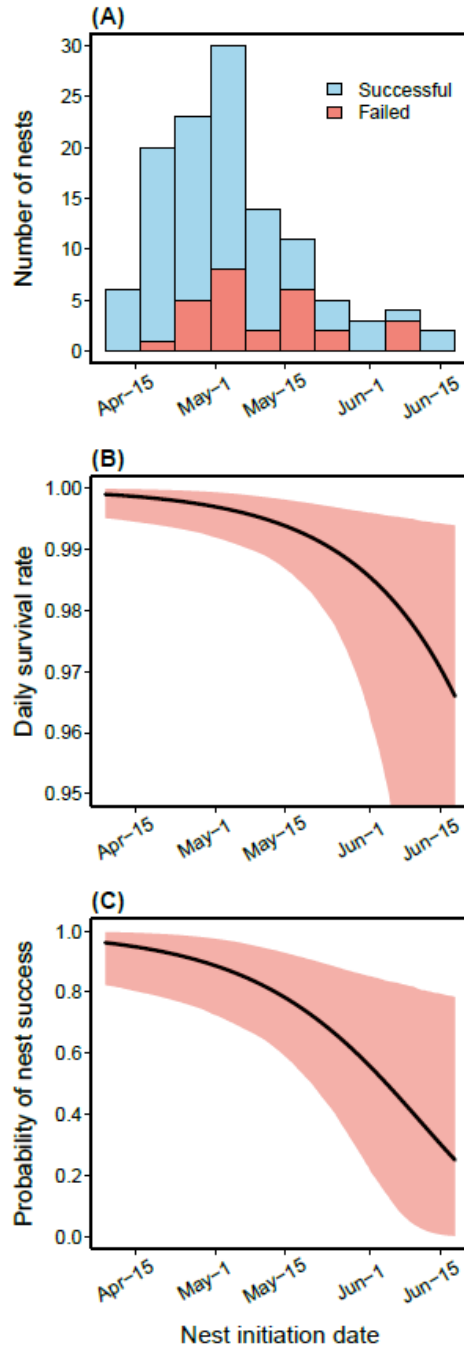


Figure 4. (A) summarizes nest initiation dates from 118 Black-backed Woodpecker nests in post-fire forests, split between successful and failed nests. Line plots show (B) predicted daily survival rate, and (C) overall probability of nest success as a function of nest initiation date. Mean relationships are shown as black lines and shaded regions depict 95% credible intervals. Predictions are shown from the best supported nest survival model.

Supplemental Material

Supplement to:

Stillman, A. N., Siegel, R. B., Wilkerson, R. L., Johnson, M., Howell, C. A., & Tingley, M. W. (2019). Nest site selection and nest survival of Black-backed Woodpeckers after wildfire. *The Condor: Ornithological Applications*, **121**, duz039.

Corresponding author:

Andrew N. Stillman

Ecology & Evolutionary Biology, University of Connecticut, Storrs, CT

Phone: +1 (860) 486-5522.

Email: andrew.stillman@uconn.edu

Table S1. Additional information on six wildfires where we monitored Black-backed Woodpecker nests between 2011 and 2018. Burn severity is shown as the percent change in canopy cover from pre-fire to immediately after fire, binned into four severity categories (0–24%, 25–49%, 50–74%, 75–100% change in canopy cover). Pre-fire habitat type is presented as the dominate California Wildlife Habitat Relationships (CWHR) classification within the fire area. Definitions of each habitat classification are provided at <https://www.wildlife.ca.gov/Data/CWHR/Wildlife-Habitats>.

Fire name	National forest name	Ignition date	Fire size (ha)	Burn severity proportion by class		Dominant pre-fire habitat type (CWHR)
Peterson	Lassen	6/21 2018	3307	0–24%:	0.52	Eastside Pine (EPN)
				25–49%:	0.12	
				50–74%:	0.10	
				75–100%:	0.27	
Sugarloaf	Lassen	8/1 2009	3864	0–24%:	0.24	Ponderosa Pine (PPN)
				25–49%:	0.12	
				50–74%:	0.11	
				75–100%:	0.54	
Wheeler	Plumas	7/5 2007	9484	0–24%:	0.23	Sierra Mixed Conifer (SMC)
				25–49%:	0.09	
				50–74%:	0.10	
				75–100%:	0.58	
Moonlight	Plumas	9/3 2007	26509	0–24%:	0.27	Sierra Mixed Conifer
				25–49%:	0.08	
				50–74%:	0.08	
				75–100%:	0.56	
Chips	Plumas/Lassen	7/28 2012	31114	0–24%:	0.63	Sierra Mixed Conifer, White Fir (WFR)
				25–49%:	0.08	
				50–74%:	0.06	
				75–100%:	0.23	
Bald	Lassen/Shasta	7/30 2014	16258	0–24%:	0.21	Eastside Pine
				25–49%:	0.12	
				50–74%:	0.12	
				75–100%:	0.55	

Table S2. Summary of field sampling effort for Black-backed Woodpecker nests in six post-fire areas of northern California, showing the number of nests monitored and the total number of observation intervals (i.e. the period between consecutive nest visits) recorded for each fire-year combination.

Fire name	Year	Time since fire (years)	Nests	Observation intervals
Peterson	2011	3	5	40
Sugarloaf	2011	2	6	33
Wheeler	2012	5	12	73
	2013	6	9	159
Moonlight	2014	7	13	134
	2015	8	15	148
	2016	9	9	93
	2017	10	13	55
Chips	2017	5	10	35
	2018	6	10	67
Bald	2017	3	8	61
	2018	4	8	58
Total:	2011–2018	2–10	118	956

Table S3. We created a set of 14 candidate models based on hypotheses about Black-backed Woodpecker nest survival relationships in post-fire forests. We grouped model covariates into three categories (habitat characteristics, nest tree characteristics, and abiotic/temporal variables) and evaluated every combination of these three groups. We also tested specific hypotheses regarding different mechanisms of nest survival risk, including predation, temperature/weather extremes, and nest abandonment due to low foraging success or cavity eviction. Models are shown in order of increasing LOOIC to facilitate comparisons to Table 2 in the main text. WAIC (Widely Applicable Information Criterion) model selection results are shown for the 14 candidate models, with Δ WAIC given as the difference between each candidate model and the model with the lowest WAIC. WAIC values were calculated using pointwise log-likelihood values from 4500 posterior draws.

Model covariates	Hypothesis and rationale	WAIC	Δ WAIC
Initiation date + Nest day	Temporal factors alone influence nest survival.	283.23	0
Initiation date + Nest day + Temp anomaly	Abiotic/temporal factors influence nest survival.	286.12	2.89
Intercept only	Nest survival is random with regards to the habitat characteristics, nest characteristics, and abiotic/temporal characteristics that we measured (null model).	285.50	2.27
Initiation date + Snag count + Burn severity + Distance to edge + Time since fire	Habitat characteristics, as well as initiation date, influence nest survival.	291.15	7.92
Initiation date + Tree DBH + Cavity height + Orientation	Nest characteristics, as well as initiation date, influence nest survival.	294.64	11.41
Burn severity + Time since fire	Burn severity and time since fire, which are potential indicators of foraging habitat quality, influence nest survival.	292.15	8.92
Tree DBH + Cavity height + Orientation	Nest characteristics influence nest survival.	292.41	9.18
Cavity height + Distance to edge	Cavity height and distance to patch edge, which reflect potential predation risk, influence nest survival.	296.00	12.77
Initiation date + Nest day + Temp anomaly + Snag count + Burn severity + Distance to edge + Time since fire	Abiotic/temporal factors and habitat characteristics, but not nest characteristics, influence nest survival.	300.68	17.45

Initiation date + Nest day + Temp anomaly + Tree DBH + Cavity height + Orientation	Abiotic/temporal factors and nest characteristics, but not habitat characteristics, influence nest survival.	304.74	21.51
Cavity height + Distance to edge + Time since fire + Nest day	Predation risk increases with time since fire and decreases with distance to edge and increasing cavity height. Older nests, which have more vocal nestlings, will have a higher predation risk.	300.11	16.88
Snag count + Burn severity + Distance to edge + Time since fire	Habitat characteristics influence nest survival.	302.27	19.04
Snag count + Burn severity + Distance to edge + Time since fire + Tree DBH + Cavity height + Orientation	Habitat characteristics and nest characteristics, but not abiotic/temporal variables, influence nest survival.	301.19	17.96
Initiation date + Nest day + Temp anomaly + Snag count + Burn severity + Distance to edge + Time since fire + Tree DBH + Cavity height + Orientation	All habitat characteristics, nest characteristics, and abiotic/temporal characteristics that we measured influence nest survival (global model).	311.53	28.3

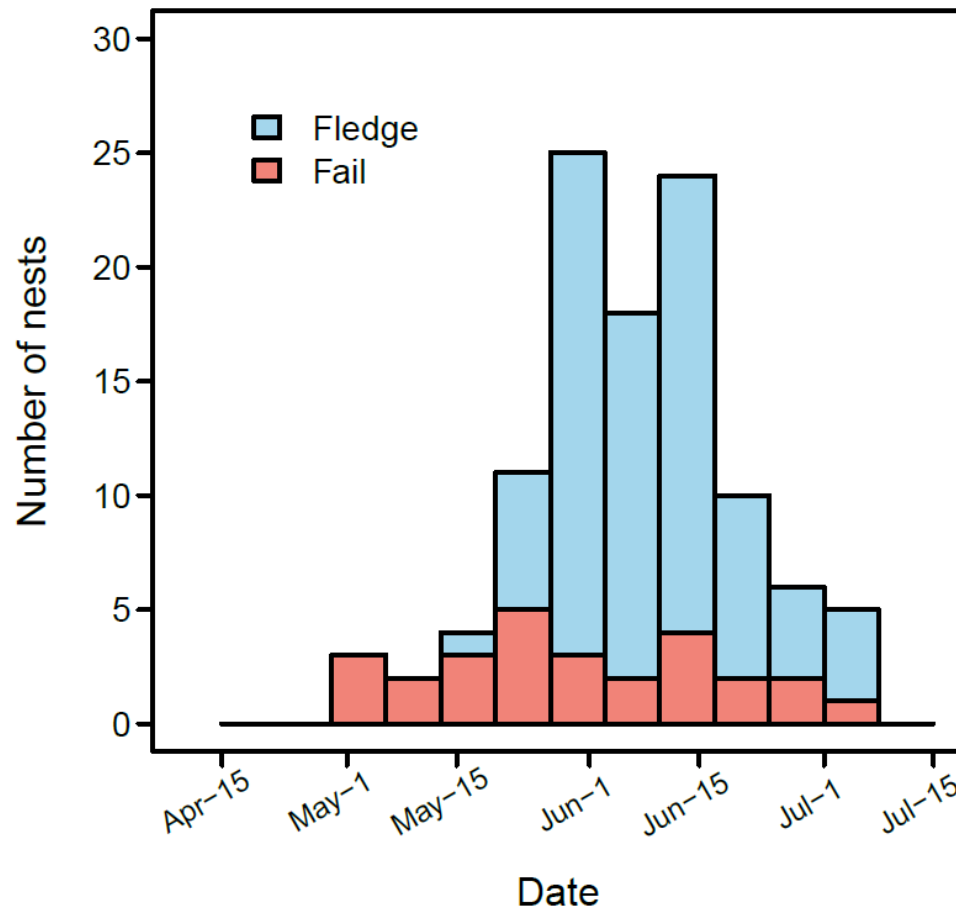


Figure S1. Fledging dates (at least one young permanently left the nest) and nest failure dates (nest confirmed depredated or abandoned) for Black-backed Woodpecker nests in northern California. Out of 118 nests, 81 fledged successfully, 27 failed, and 10 had an undetermined fate.

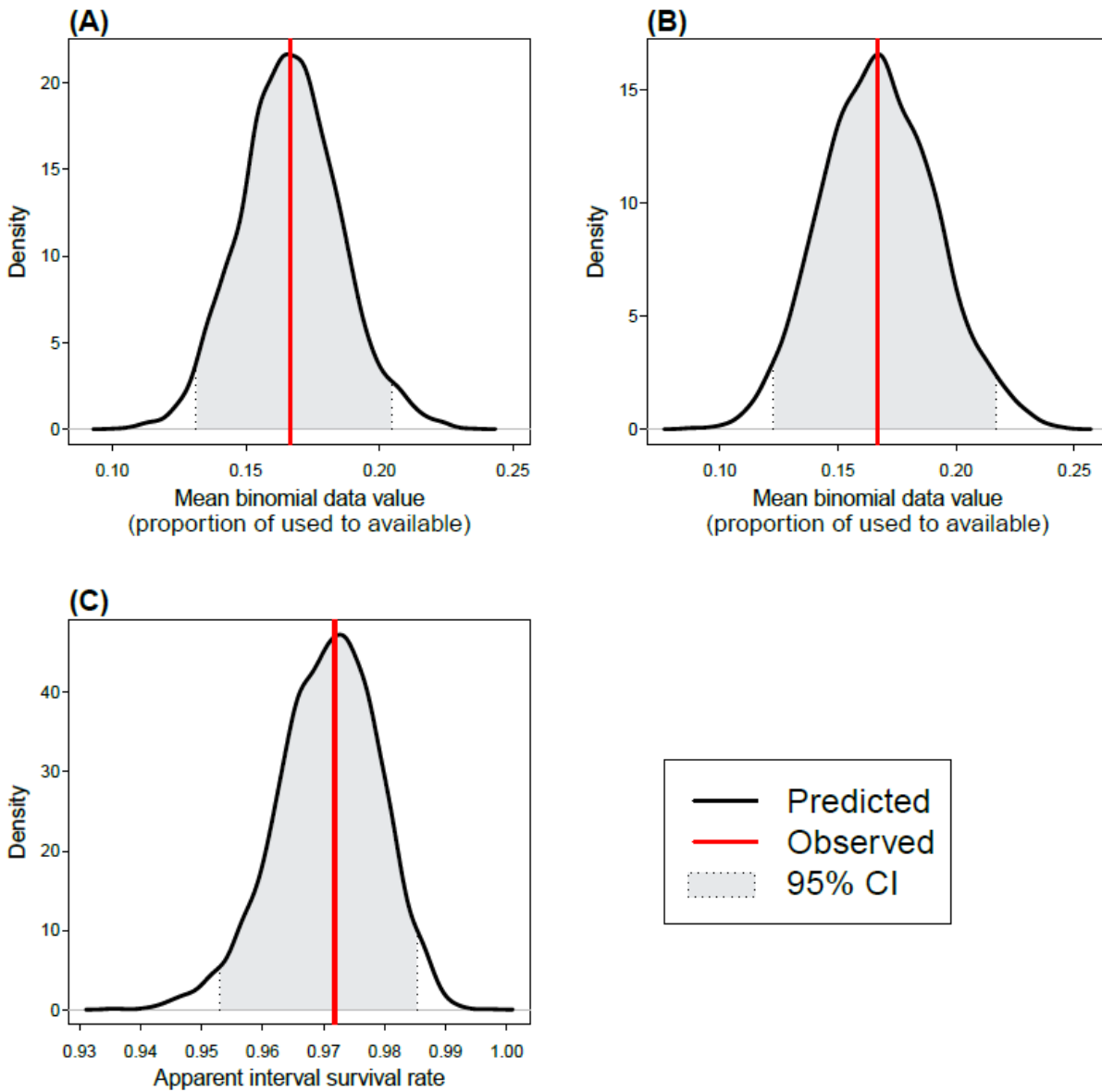


Figure S2. Posterior predictive checks indicated no evidence for lack of model fit for (A) the model of woodpecker nest stand selection, (B) the model of nest tree selection, and (C) the model of daily nest survival probability. A test statistic was created for each model based on the mean value of the observed response variable, which represents the ratio of used to available points in (A) and (B), and the apparent interval survival rate in (C). Red lines depict the observed value of the test statistic and solid black lines give the distribution of model-derived estimates with shaded 95% confidence intervals.

Chapter 2:

Age-dependent habitat relationships of a burned forest specialist emphasize the role of pyrodiversity in fire management

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Stillman, A. N., Siegel, R. B., Wilkerson, R. L., Johnson, M., & Tingley, M. W. (2019). Age-dependent habitat relationships of a burned forest specialist emphasize the role of pyrodiversity in fire management. *Journal of Applied Ecology*, **56**, 880–890.

ABSTRACT

1. Variation in fire characteristics, termed pyrodiversity, plays an important role in structuring post-fire communities, but little is known about the importance of pyrodiversity for individual species. The availability of diverse post-fire habitats may be key for fire-associated species if they require different resources at different life history stages.

2. We tested for age-specific habitat relationships in the black-backed woodpecker, a post-fire specialist. We used radio-telemetry to track fledgling and adult woodpeckers in burned forests and built resource selection functions to compare the effect of stand-, tree-, and snag-level covariates between adults and fledglings.

3. Fledgling black-backed woodpeckers selected habitat with more live trees than adults, and used more heterogeneous habitats burned at lower severity, illustrating strong age-dependent effects on habitat selection. Within selected stands, fledglings were less likely to use snags and more likely to use live trees when compared to adults, but both age classes showed strong positive selection for larger-diameter trees (live and dead). Over the 60 days after leaving their nests, fledglings showed an increasing propensity to use snags rather than live trees.

4. Our results provide evidence that the predation–starvation hypothesis, which posits a trade-off between foraging efficiency and the need to minimize predation risk, plays a role in structuring the age-dependent habitat use of a burned forest specialist. Adult black-backed woodpeckers selected resources associated with food availability, but these resources occurred in relatively open, exposed habitat. Fledglings selected habitat that provided increased cover, perhaps as a strategy to reduce predation risk.

5. *Synthesis and applications.* Globally, fires are increasing in severity and extent, leading to increased focus on fire-associated species that play keystone roles in facilitating biodiversity

resilience. Our findings suggest that a diversity of patches burned at different severities may benefit post-fire specialists like the black-backed woodpecker at multiple life history stages. The increasing prevalence of large, homogeneously high-severity “megafires” may present an emerging threat even to post-fire specialists, and we urge land managers to consider opportunities to promote pyrodiversity in the face of novel fire regimes.

INTRODUCTION

Wildfire is a key ecological disturbance in forests worldwide, generating successional mosaics of habitat that structure biotic communities (Kelly & Brotons 2017). Variation in fire regime characteristics—termed pyrodiversity—creates heterogeneous post-fire habitat, which has been correlated with increased biodiversity in a variety of fire-prone systems (Tingley *et al.* 2016a; Beale *et al.* 2018). Mounting evidence in support of this ‘pyrodiversity–biodiversity’ hypothesis has made promoting and retaining fire heterogeneity an increasingly influential guiding principal in forest management and biodiversity conservation (Kelly, Brotons & McCarthy 2017). Pyrodiversity is generally believed to foster biodiversity where fire regimes yield heterogeneous patchworks of different habitats, each with its own affiliated species (Tingley *et al.* 2016a). In this view, individual species do not benefit from pyrodiversity, as species diversity is simply an emergent property of a diversity of habitats. However, the implicit view that individual species are monolithic in their habitat requirements—depending on just one component of a diverse landscape—may not be accurate (Bolnick *et al.* 2002; Holtmann *et al.* 2017). In particular, pyrodiversity could hold substantial benefits for populations within a single species if individuals require different habitat characteristics across their full life cycle.

Globally, the size and intensity of wildfires is on the rise (Stephens *et al.* 2014). In western North America, historical fire suppression and a changing climate increasingly push the region into a novel fire regime, which is characterized by exceptionally large, homogeneously high-severity fires (Miller & Safford 2012; Stevens *et al.* 2017). These trends have led to increased focus on fire-associated species that benefit from fire and play keystone roles in facilitating biodiversity resilience. High severity fire creates dense stands of standing dead trees (snags) that may contribute to the regional persistence of deadwood-associated species including cavity-nesting birds, saproxylic insects, and cavity-using mammals (DellaSala *et al.* 2014; Hutto *et al.* 2016). The black-backed woodpecker (*Picoides arcticus*) is a post-fire specialist that appears closely tied to areas burned at high severity across much of its range (Hutto 2008). Black-backed woodpeckers depend on snags for nest sites and foraging (Seavy, Burnett & Taille 2012; Rota *et al.* 2015). In the western U.S., the species primarily feeds on the larvae of wood-boring beetles (Cerambycidae and Buprestidae), which reproduce in dead and dying trees, especially after fire (Murphy & Lehnhausen 1998). High densities of black-backed woodpeckers within recently burned areas contrast with the species' rarity in the surrounding matrix of unburned forest (Hutto 2008). It is thus reasonable to hypothesize that the black-backed woodpecker, as a flagship for biodiversity conservation in burned forests, may benefit from trends toward increasing forest fire severity.

In birds, species-specific benefits of pyrodiversity may arise from differences in the habitat requirements of adults and fledglings, particularly where a trade-off exists between foraging efficiency and the need to minimize predation risk (Houston, McNamara & Hutchinson 1993). This “predation–starvation” hypothesis may help explain foraging behaviour of birds and the ways that individuals adjust habitat selection based on perceived predation risk (Bonter *et al.*

2013). Past studies of habitat selection have indicated that some fledgling passerines select habitat with greater cover than adults, likely providing increased protection from predators (King *et al.* 2006; Jones, Brawn & Ward 2017). Habitat use in adult black-backed woodpeckers is linked to areas with high food availability (Tingley *et al.* 2014; Rota *et al.* 2015), yet open, snag-dominated stands containing high food concentrations often have less cover than surrounding areas. Fledgling woodpeckers generally do not forage for themselves during the period when they are dependent on food provisioning from adults. Thus, fledgling black-backed woodpeckers may exhibit different habitat relationships than adult black-backed woodpeckers, even while using burned forests.

We studied differences between habitat selection in adult and fledgling black-backed woodpeckers in burned forests. Specifically, we addressed three predictions that stem from the predation–starvation hypothesis. First, we predicted that adult black-backed woodpeckers would select habitat that is associated with the availability of key resources for adults, including nest sites and food availability. We therefore predicted that adults would show strong relationships with snag density and areas burned at relatively high severity. Second, because young fledglings are provisioned by their parents, we predicted that fledglings would select habitat associated with higher cover than adults. In burned forests, higher cover is generally available in areas burned at relatively low severity, with abundant live trees remaining after fire. Third, we predicted that fledgling habitat use would shift to include more snags as fledglings aged and became more independent from parents. Our objective was to examine the role of pyrodiversity across life stages of a burned forest specialist in light of the predation–starvation trade-off. In addition, we sought to provide relevant information to forest managers interested in maintaining habitat for black-backed woodpeckers and other species associated with burned forests.

MATERIALS AND METHODS

STUDY AREA

We conducted our research within forests burned by six wildfires in Plumas and Lassen National Forests of northeastern California: Moonlight (burned in 2007), Wheeler/Antelope Complex (2007), Peterson Complex (2008), Sugarloaf/Hat Creek Complex (2009), Chips (2012), and Bald (2014). Study areas ranged from 2–10 years post-fire at the time of data collection. Four of the fires (Moonlight, Wheeler, Sugarloaf, and Chips) burned predominately Sierran mixed conifer forest dominated by *Pinus ponderosa*, *P. jeffreyi*, *Abies concolor*, *A. magnifica*, *Pseudotsuga menziesii*, and *Calocedrus decurrens*. The Peterson and Bald fires burned mostly eastside pine forest composed of *P. ponderosa*, *P. jeffreyi*, *C. decurrens*, and *Juniperus occidentalis*.

WOODPECKER CAPTURE AND TRACKING

We used radio-telemetry to track the movements and habitat use of adult and fledgling black-backed woodpeckers. During the breeding season between 2011 and 2016, we tagged adult woodpeckers in the Moonlight, Wheeler, Peterson, and Sugarloaf fires. In 2016 and 2017, we tagged fledgling woodpeckers in the Moonlight, Chips, and Bald fires. Adults were captured in mist nets or at the nest with hoop nets. To prevent nest abandonment, adults were only captured with hoop nets if nestlings were at least 5 days old. We captured nestlings 1–3 days before fledging using the hole-saw method and replaced all nestlings back into the cavity immediately after processing (Ibarzabal & Tremblay 2006). Between 2011 and 2016, we attached a 1.6–2.0-g VHF radio transmitter (Model BD-2, Holohil Systems, Carp, Ontario, Canada) to the dorsal surface of an inner rectrix feather for each bird using two loops of monofilament and a thin layer

of ethyl cyanoacrylate. In 2017, fledglings were fitted with a 1.6-g programmable connectivity tag (Model CTx Ag 392, Lotek Wireless Inc., Newmarket, Ontario, Canada) using the leg-loop harness method secured with elastic beading cord (Rappole & Tipton 1991). All individuals were fit with a unique combination of colour bands and a numbered USGS leg band. Transmitters weighed less than 3% of average body mass for adult woodpeckers (mean mass = 67.5g) and fledgling woodpeckers (mean mass = 61.7g) in accordance with recommended practices to minimize transmitter impact on bird behaviour (Fair, Paul & Jones 2010).

We tracked adult and fledgling woodpeckers between April and August each year, attempting to locate each bird at least once every three to five days. Individuals were located using radio receivers and Model RA-7/Model RA-14K antennas (Telonics Inc., Mesa, Arizona, USA). Once found, each bird was followed on foot by a team of paired observers for at least one hour, or until the bird landed on and “used” a maximum of 20 trees. Black-backed woodpeckers were unwary of observer presence during tracking bouts and did not visibly alter their behaviour, even when observed at a distance of 3–4 m (Tingley *et al.* 2014; Rota *et al.* 2015). However, observers attempted to remain at least 10 m away from tagged birds while still maintaining a direct line of sight to record behaviour.

HABITAT USE MEASUREMENTS

For adult woodpeckers, we defined “used habitat” as each tree where the woodpecker landed, remained for at least 5 s, and interacted with the tree using one of the following common behaviours: pecking, gleaning, probing, flaking, or excavating. We found that adult woodpeckers exhibited these behaviours on nearly every tree on which they landed. We used a 5-second minimum threshold for “use” to omit trees on which woodpeckers stopped only momentarily while travelling between habitat patches. More details on adult tracking methods can be found in

Tingley et al. (2014). In contrast, fledgling black-backed woodpeckers tended to be more sedentary than adults, and they did not show the same propensity to forage on every tree on which they landed. Thus, we modified our definition of habitat “use” by fledglings to include all trees that a fledgling landed on and remained for at least 5 s. This definition of “use” omits the trees that fledglings landed on only briefly while travelling between habitats, but allows for the inclusion of trees used as daytime roost sites.

During each tracking bout, we marked each used tree with a numbered pin flag and recorded geographic coordinates (UTM) using a handheld GPS. We also recorded behavioural observations and the duration a woodpecker remained on each tree. After completing a tracking bout, we returned to flagged trees to record tree characteristics and measure surrounding habitat. We recorded species of each used tree, plus diameter at breast height (DBH), and whether the tree was alive or dead. For dead trees only, we also estimated the percent of bark remaining (aggregated into four categories: 0–10%, 11–50%, 51–90%, >90%) and counted the number of wood-boring beetle exit holes (four categories: 0–10, 11–20, 21–50, and >51) on the trunk between 0–1 m above ground as an index of past beetle activity. We measured the tree density surrounding used trees by counting the number of snags and live trees with DBH > 10 cm within a 10-m radius. We assigned burn severity within a 50-m radius to one of four categories (Unburned, Low, Medium, High) based on the estimated percent of canopy mortality (0, <25, 26–80, >80%, respectively).

In addition to habitat variables collected in the field, we used data from the Rapid Assessment of Vegetation Condition after Wildfire program (<https://www.fs.fed.us/postfirevegcondition/index.shtml>) to extract the percent change in canopy cover from pre-fire to immediately after fire at each use location (hereafter ‘point’). We used this measure of burn

severity to create an index of pyrodiversity by calculating the standard deviation of burn severity within a 100-m radius of each point (Tingley *et al.* 2016a).

SYSTEMATIC HABITAT MEASUREMENTS

Our inference in this study centred on the relative probability of resource use for adult versus fledgling back-backed woodpeckers. Habitat use is considered selective when certain resources are used disproportionate to their availability (Manly *et al.* 2002), but biologically arbitrary definitions of “available resources” can lead to bias when estimating resource selection parameters (Jones 2001). Here, we used the Design III method, where a unique distribution of used and available habitat samples are collected for each tagged individual (Manly *et al.* 2002). This design was appropriate because we tracked woodpeckers across multiple fires and regions within fires, so available habitat differed between individuals.

We used a minimum convex polygon (MCP) bounding the tracking locations of each bird to define the habitat that was available for use, and we measured habitat variables at systematically spaced points on a 100-m by 100-m grid covering the MCP. We did not measure available habitat for birds with fewer than 10 tracking points. For adult woodpeckers, we collected stand-level measurements (i.e., tree density, burn severity) at alternating points in the grid, but collected tree-level measurements (i.e., size, condition, species, snag decay, beetle exit holes) at every point in the grid. To build a sample of available trees, we collected data on the snag and live tree closest to each grid point, but within 50 m. For fledgling woodpeckers with MCP > 200 ha, we randomly discarded gridded survey points prior to sampling until the ratio of used points to available points was 1:3.

STATISTICAL ANALYSES

Statistical inference was made in three steps. First, we tested the statistical hypothesis that patterns of habitat use are different between woodpecker age classes using t-tests for normally distributed samples, and Mann-Whitney U-tests or chi-squared tests for non-normal data. This preliminary analysis provided a baseline description of habitat use before accounting for availability. Second, we analysed our use-availability data using three resource selection functions, each built at a different scale of selection: stand selection, tree selection (live trees and snags), and snag selection. These models only employed data from birds where we measured available vegetation in a systematic grid. Because we were interested in characterizing the habitat relationships of fledgling woodpeckers during the stage when they are dependent on parental provisioning, we included fledgling use points collected only within the first 35 days after fledging. Field observations indicated that fledglings became independent from parental provisioning after about 35 days.

We built resource selection functions in a framework that accounts for the possibility that some points in our available sample may have been used by woodpeckers outside of observation periods, a problem termed “zero-contamination” (Lele & Keim 2006; Lele 2009). Models employed an unbalanced matching design, where all individuals are included within a single model for each scale of selection, but every used point is compared against the unique set of available points surveyed within the individual’s MCP (Lele, Keim & Solymos 2017). In each of the three models, we included an interaction of age class on every covariate — the coefficient of this interaction term provides a statistical test of whether fledgling selection differs from adults for each variable.

We tested alternative link functions for each model by building exponential, logistic, probit, and complementary log-log models, and selected the functional form which resulted in

the lowest Akaike Information Criterion (ΔAIC) (Lele & Keim 2006). The complementary log-log resource selection probability function provided the best fit for all three models, and we used this functional form in subsequent analysis.

For our stand-level model, we included four covariates of resource use: live tree density, snag density, burn severity (*in situ* measurement), and σ of burn severity (a measure of pyrodiversity). As we expected the effect of incremental increases in tree density to attenuate at higher densities, we log-transformed both tree count variables.

For our tree-level model, we modeled the relative probability of use for each tree as a function of tree diameter (DBH), whether the tree was alive or dead, and tree species. We included tree species as a series of four dummy variables based on the following groupings: *Pinus* (pines), *Abies/Pseudotsuga* (white fir, red fir, and Douglas-fir), *Calocedrus* (incense cedar), and all other non-dominant species.

For our snag-level model, we modelled the relative probability that a woodpecker would use a snag as a function of DBH, the amount of bark remaining (which we considered an index of snag decay), and the number of wood-boring beetle exit holes on the lowest meter of trunk. We included the categorical estimate of percent bark remaining as a continuous variable with values 1–4. For the number of beetle exit holes, we assigned each category (0–10, 11–20, 21–50, and >51) integers between 1–4; including these data as a continuous variable reflected our observation that the underlying relationship between beetle holes and woodpecker use was log-linear (Fig. S1). In all three models, we centred and standardized continuous covariates to aid comparisons between coefficient estimates.

We evaluated our resource selection models using a 5-fold cross validation technique designed for presence/available data (Boyce *et al.* 2002). To create training/test data, we

iteratively withheld 20% of the used and available points for each bird, without replacement. We assessed model performance by examining Spearman rank correlations between predicted values, divided into 10 equally-sized bins, and area-adjusted frequencies. Strong positive correlations and low p-values ($p < 0.05$) indicate good predictive performance of a model (Boyce *et al.* 2002).

Finally, we examined the effect of fledgling age on the probability of snag use to test the prediction that fledgling woodpeckers gradually shift resource use as they become independent from adult provisioning. We built a binomial mixed-effects model to examine the effect of fledgling age, measured as days since fledging, on the logit-transformed probability of snag use. We included a random slope for each individual to account for repeated observations of fledglings. All analyses were performed in R version 3.5.1 using the packages lme4 (Bates *et al.* 2014) and ResourceSelection (Lele 2009; Lele, Keim & Solymos 2017; R Core Team 2018).

RESULTS

We recorded habitat use data for 49 adult and 22 fledgling black-backed woodpeckers between 2011 and 2017, and we sampled available habitat for 41 adults and 15 fledglings. Overall, we characterized used habitat at 5,352 adult points and 915 fledgling points, and we measured 4,242 and 1,896 available points for adults and fledglings, respectively.

HABITAT USE

Patterns of habitat use differed between adult and fledgling black-backed woodpeckers. Adults tended to use areas burned at medium or high severity, but fledglings showed proportionally greater use of habitat burned at medium and low severity (Fig. 1, Fig. 2). Even within large patches of forest burned at relatively high severity, fledglings tended to associate

with small “island” patches of lower burn severity or boundaries between high and low severity burn stands (Fig. 1). Fledglings used areas with significantly greater variation in burn severity within a 100-m radius than adults ($t = -2.03$, $df = 1119.3$, $p < 0.01$; Fig. 2). The percent change in canopy cover pre-fire to post-fire was significantly lower for fledgling ($38.33 \pm 1.30\%$) than adult woodpeckers (adult mean = $64.05 \pm 0.53\%$; $U = 1411000$, $p < 0.001$). This pattern was strongest during the first 10 days after fledglings left the nest. Woodpeckers tended to nest in high severity stands, but newly fledged young generally left the nest stand and associated with surrounding areas of low and medium burn severity, where they sought daytime roost sites in or near live trees and received provisioning from adults. During 84 hours of fledgling behavioural observations, individuals between 0 and 10 days post-fledge spent 26.6% of their time in habitat classified as low severity from field-based assessment, compared to 15.1% for fledglings over 20 days post-fledge, and 7.1% for adults (based on 213 observation hours).

Vegetation measurements at used points showed further differences in habitat use between adults and newly fledged birds. On average, fledglings used areas with lower snag density ($t = 14.92$, $df = 1324.3$, $p < 0.001$) and higher live tree density ($t = -11.42$, $df = 1144.6$, $p < 0.001$) than adults (Fig. 2). Both adults and fledglings used snags more frequently than live trees, but fledglings used a greater proportion of live trees than adults ($\chi^2 = 358.87$, $df = 1$, $p < 0.001$; Fig. 2). The mean DBH of trees used by fledgling woodpeckers was 44.4 cm, compared to a mean DBH of 39.2 cm for adults ($t = -6.35$, $df = 1097.5$, $p < 0.001$). Both adult and fledgling woodpeckers primarily used fir and pine trees, which in our study areas included white fir, red fir, Douglas-fir, ponderosa pine, and Jeffrey pine.

Fledglings showed changing habitat preferences with time since fledging. The probability of a fledgling using a snag increased with the number of days since the fledgling left the nest

(odds ratio: 1.03, 95% CI: (1.01,1.06), $p = 0.014$, Fig. S2). Thus, the odds of a three-week old fledgling using a snag were two times greater than a one-day old fledgling.

RESOURCE SELECTION

We used resource selection functions to estimate the effect of stand-, tree-, and snag-level characteristics on the relative probability of woodpecker resource use while accounting for availability. The sample size of used/available points was 6,132/3,969, 5,818/6,416, and 4,733/5,724 for the stand-, tree-, and snag-level models, respectively.

Among stand-level characteristics, snag density had an important effect on the relative probability of use for both fledglings and adults (Table 1). For example, a point with 10 snags within a 10-m radius was five times more likely to be used by adults than a point with one snag (Fig. 3). Live tree density also had a positive effect on both adult and fledgling stand use, but this effect was significantly stronger in fledglings (Table 1). Plots of fitted probabilities showed that fledglings had the highest relative probability of use in stands burned at medium severity and lowest relative probability of use in stands burned at high severity (Fig. 3), although after accounting for tree density, the fledgling relationship to high severity did not differ from adults (Table 1). By comparison, adults showed high relative probability of use in stands burned at both medium and high severity (Fig. 3) but selected low and medium severity significantly less than fledglings (Table 1). In addition, both age classes demonstrated a significant positive relationship with burn severity heterogeneity; this relationship was stronger in fledglings (Table 1).

The resource selection model of tree covariates demonstrated further differences between adults and fledglings. Adult black-backed woodpeckers showed significantly stronger selection for snags than fledglings, and both selected trees with greater DBH. Across age classes, relative probability of use was substantially greater for fir and pine trees compared to incense cedar and

non-dominant species, although fledglings showed significantly greater selection of incense cedar than adults (Table 1, Fig. 4).

Fledglings and adults also showed differential selection in the types of snags used (Table 1). Both age classes selected snags with larger DBH, but this relationship was significantly stronger in adults. Relative probability of use also decreased with increased snag decay. Adult woodpeckers alone, however, showed a significant, positive relationship between snag usage and the number of wood-boring beetle exit holes present (Table 1).

MODEL EVALUATION

Using five-fold cross validation, area-adjusted frequencies were positively correlated with resource selection function predictions for all three models. Spearman rank correlations between area-adjusted frequency and binned model predictions ranged from 0.952 to nearly 1, providing no evidence for lack of model fit or poor model performance (mean $r_s = 0.980$, $p < 0.001$).

DISCUSSION

Information on wildlife-habitat relationships in burned forests is key to understanding the potential effects of changing fire regimes on wildlife in fire-prone systems and the implications of post-fire forest management practices. We tested three predictions regarding (1) habitat selection in adult black-backed woodpeckers, (2) habitat selection in fledglings, and (3) change in habitat use as fledglings grew older. Our results demonstrated clear differences between adult and fledgling habitat and highlight the role of pyrodiversity in fire management. Adult black-backed woodpeckers selected stands burned at high or medium severity and with high snag density, and they preferentially used snags relative to live trees. In contrast, fledgling black-

backed woodpeckers selected stands burned at medium to low severity and did not show strong selection for snags over live trees. We also found that the probability of fledglings using snags increased as fledglings grew older.

Fledgling black-backed woodpeckers positioned their natal home ranges in areas that, in general, incorporated more live trees when compared to adults (Fig. S3). This trend meant that the baseline distribution of available habitat differed between adults and fledglings due to selection at the home range scale (second-order selection; Johnson 1980). To show evidence of selection in our analysis, a woodpecker additionally needed to display disproportionate use of a habitat relative to its availability to that individual. Thus, we assessed selection of resources from within the home range and not selection of the home range itself, leading to conservative estimates of the differences between adults and fledglings. It is important to note that even within home ranges dominated by low burn severity, we still found that fledglings selected areas associated with tree cover and avoided high burn severity patches.

Black-backed woodpeckers are known for their strong association with high and medium severity burned forests in western North America (Hutto 2008), but our results indicate that landscape-level pyrodiversity plays a key role in meeting the habitat requirements of black-backed woodpeckers across life history stages. Maps of woodpecker space use revealed a tendency for woodpeckers to use edge areas between high and low-severity patches of burned forest (Fig. 1), and both age classes demonstrated a positive relationship between habitat use and burn severity variation. This pattern may arise from the need for fledglings and adults to maintain proximity to each other (e.g., for provisioning) while still selecting for different habitat characteristics.

Resource selection functions for snag use indicated that adult black-backed woodpeckers selected snags that were larger in diameter, exhibited relatively less bark decay, and showed greater sign of past beetle activity. These results are consistent with findings based on adult black-backed woodpeckers in eastern Canada, which showed preference for larger, less deteriorated snags (Nappi *et al.* 2003). In our study, fledgling woodpeckers also showed positive relationships with snags that were larger and less deteriorated, but evidence of past beetle emergence did not have a significant influence on snag selection. The ratio of snag use to live tree use gradually increased in older fledglings, even while they were still dependent on parental provisioning. Our field observations indicated that this might be due to fledglings spending an increasing amount of time accompanying parents on foraging trips as they grew older.

The predation–starvation hypothesis provides theoretical support for the importance of pyrodiversity in meeting habitat needs across life stages of black-backed woodpeckers in burned forests. Foraging woodpeckers encounter the highest densities of wood-boring beetle larvae, their primary food source, in areas characterized by high snag density resulting from high-severity fire. However, these “snag forests” are open, exposed habitats (DellaSala *et al.* 2014); woodpeckers using these areas may incur higher risks of predation from aerial predators such as hawks. Young fledgling woodpeckers, which are provisioned by parents, may adjust to this trade-off by selecting habitat with a greater live tree component to provide cover from overhead predators. In addition, live trees may provide thermal cover in an otherwise hot, exposed environment. Our anecdotal observations indicated that much of the time, young fledglings adopted daytime roost sites in dense stands of live trees, which served as ‘nurseries’ for the birds while provisioning parents conducted trips back and forth between the fledgling and high-severity foraging stands. The importance of fledgling access to high-cover vegetation has been

demonstrated in many passerine bird species (King *et al.* 2006; Jones, Brawn & Ward 2017); in addition, these high-cover hideouts have been implicated in higher fledgling survival rates relative to low-cover areas (Anders *et al.* 1997; King *et al.* 2006). We suggest that additional research focus on the fitness consequences of these habitat use patterns, including the relationship between selection for cover and fledgling survival.

IMPLICATIONS FOR MANAGEMENT UNDER NOVEL FIRE REGIMES

Recently, the western U.S. has experienced unprecedented increases in the size and severity of forest fires (Miller & Safford 2012; Stevens *et al.* 2017). Transitioning fire regimes are yielding increases in the frequency and extent of “megafires,” that is, large, severe wildfires >10,000 ha in extent (Stephens *et al.* 2014). These trends have generated concern over the conservation of forest species (Jones *et al.* 2016; Ganey *et al.* 2017), but the effect of more severe, more homogeneous fires on fire-associated species also needs to be considered. Past studies have provided evidence that some severe forest fire has neutral or beneficial effects on wildlife (Hutto *et al.* 2016), and black-backed woodpeckers are frequently considered a specialist on severe fires. Despite this, our results indicate that black-backed woodpecker habitat preferences vary by life stage. Consequently, heterogeneity in post-fire systems may be critical to meet habitat requirements across the full life history of this post-fire specialist. As megafires burn more homogeneously, providing less access to low and moderate severity areas juxtaposed with high severity areas (Stephens *et al.* 2014), our results suggest that shifting fire regimes may pose an emerging threat to certain post-fire specialists that thrive on pyrodiverse landscapes.

More information on the effects of megafires on wildlife populations is urgently needed, particularly regarding the potential effects of high severity fire when it occurs homogeneously over large, continuous areas. While the largest wildfire we studied comprised 30,897 ha, much of

our sampling occurred in areas characterized by moderate to high variation in burn severity instead of homogeneous high-severity landscapes. We also caution that our study does not test for differential fitness among habitats (Jones 2001), particularly whether fitness is lower in areas with more homogeneous burn severity. We recommend that future research focus on measuring the effects of pyrodiversity on fire-associated species, including links between habitat use patterns and individual fitness.

Forest fires, and the post-fire habitats that they create, can be managed in ways that promote biodiversity. Effective management strategies rely on knowledge of the characteristics of fire that enhance species' use of post-fire landscapes and the ways that variation across a fire regime can affect population dynamics (Kelly & Brotons 2017; Tingley *et al.* 2018). Our results point to the crucial need for information on the resources that structure wildlife habitat relationships beyond breeding-season adults — sound management strategies will incorporate information from full life histories. We provide novel evidence suggesting that black-backed woodpeckers may depend on mixed-severity fires to meet the needs of fledglings. Indeed, woodpecker densities within recent homogeneous megafires, such as the 102,925-ha Rim fire, fall well below predicted values based on current habitat suitability models (Tingley *et al.* 2016b). Our results suggest that these low densities may stem from low habitat heterogeneity in these fires, possibly denying adequate cover for predator avoidance by fledgling woodpeckers. The proximity of habitat burned at different severities may benefit wildlife that need heterogeneous habitat to meet different resource requirements, and we recommend that managers interested in promoting post-fire biodiversity consider the proximity of high severity stands to unburned areas and stands burned at low to medium severity.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.h5h7v20>

(Stillman *et al.* 2018).

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Table 1. Coefficient estimates, 95% confidence intervals, and p-values for factors affecting resource selection in fledgling and adult black-backed woodpeckers. Results are shown for three models representing different types of resource use: habitat use, tree use, and snag use. Main effects provide the relative selection strength for adults and interaction effects show fledgling effect relative to adults.

Covariate	Main effects (Adults)		Interaction effects (Fledgling effect)	
	Estimate	p-value	Estimate	p-value
<i>Stand model: characteristics of habitat surrounding used and available trees</i>				
Intercept	-2.23 (\pm 0.35)	< 0.001	-1.54 (\pm 1.92)	0.422
Live tree density	0.19 (\pm 0.02)	< 0.001	0.51 (\pm 0.02)	< 0.001
Snag density	1.26 (\pm 0.04)	< 0.001	0.06 (\pm 0.04)	0.434
Burn severity: High	-0.58 (\pm 0.22)	0.008	0.34 (\pm 0.41)	0.406
Medium	-0.20 (\pm 0.22)	0.375	1.26 (\pm 0.40)	0.002
Low	-0.04 (\pm 0.23)	0.874	1.36 (\pm 0.44)	0.002
Unburned	0.30 (\pm 0.26)	0.256	0.21 (\pm 0.51)	0.678
σ of burn severity	0.16 (\pm 0.02)	< 0.001	0.25 (\pm 0.05)	< 0.001
<i>Tree model: characteristics of used and available trees (live and dead)</i>				
Intercept	-5.05 (\pm 0.19)	< 0.001	2.54 (\pm 0.62)	< 0.001
DBH	1.32 (\pm 0.06)	< 0.001	-0.12 (\pm 0.21)	0.555
Snag (vs. live tree)	2.78 (\pm 0.09)	< 0.001	-2.09 (\pm 0.19)	< 0.001
Fir sp.	2.42 (\pm 0.19)	< 0.001	-0.45 (\pm 0.57)	0.430
Pine sp.	2.10 (\pm 0.18)	< 0.001	-0.23 (\pm 0.56)	0.688
Incense Cedar	-0.40 (\pm 0.23)	0.075	1.26 (\pm 0.59)	0.032

<i>Snag-only model: characteristics of used and available snags</i>				
Intercept	0.50 (\pm 0.12)	< 0.001	-1.53 (\pm 0.33)	< 0.001
DBH	2.57 (\pm 0.13)	< 0.001	-1.81 (\pm 0.36)	< 0.001
Bark decay	-0.17 (\pm 0.04)	< 0.001	-0.06 (\pm 0.10)	0.536
Beetles	0.25 (\pm 0.05)	< 0.001	-0.34 (\pm 0.11)	0.002

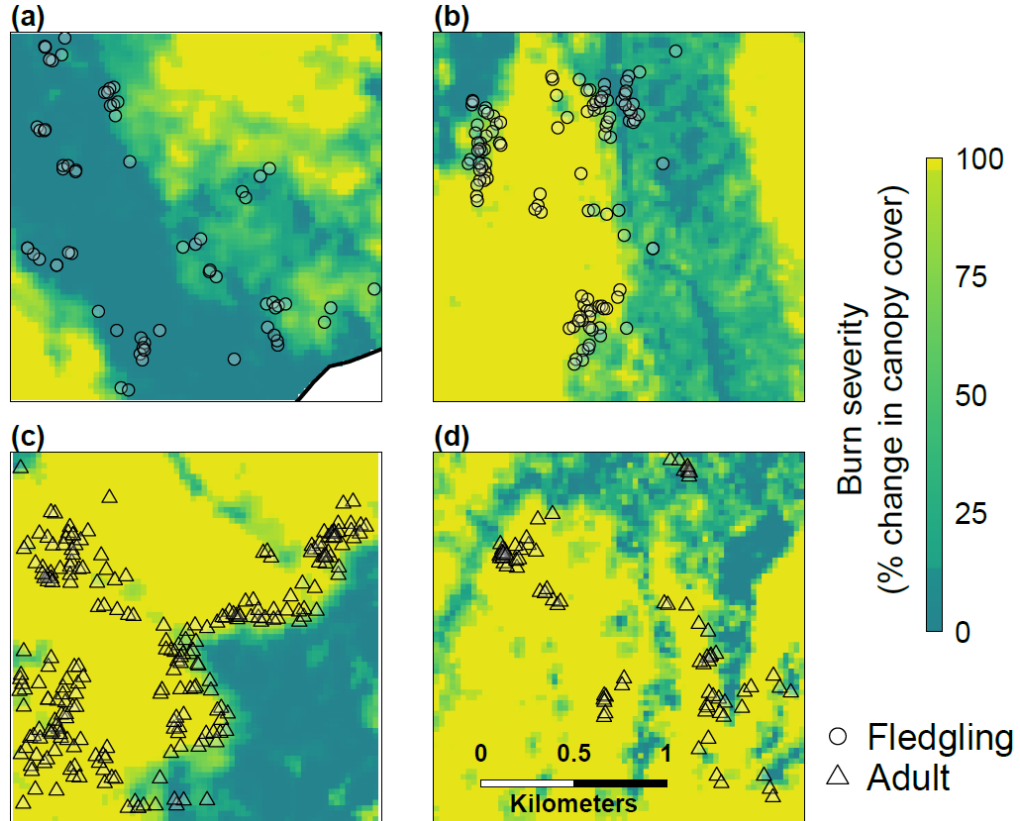


Figure 1. Example observed locations of black-backed woodpeckers in post-fire forests for fledglings in (a) the Moonlight and (b) Bald fires, and for adults in (c) the Wheeler and (d) Sugarloaf fires, demonstrating apparent juvenile preference for areas of lower burn severity (blue–green) and adult preference for areas of greater burn severity (green–yellow).

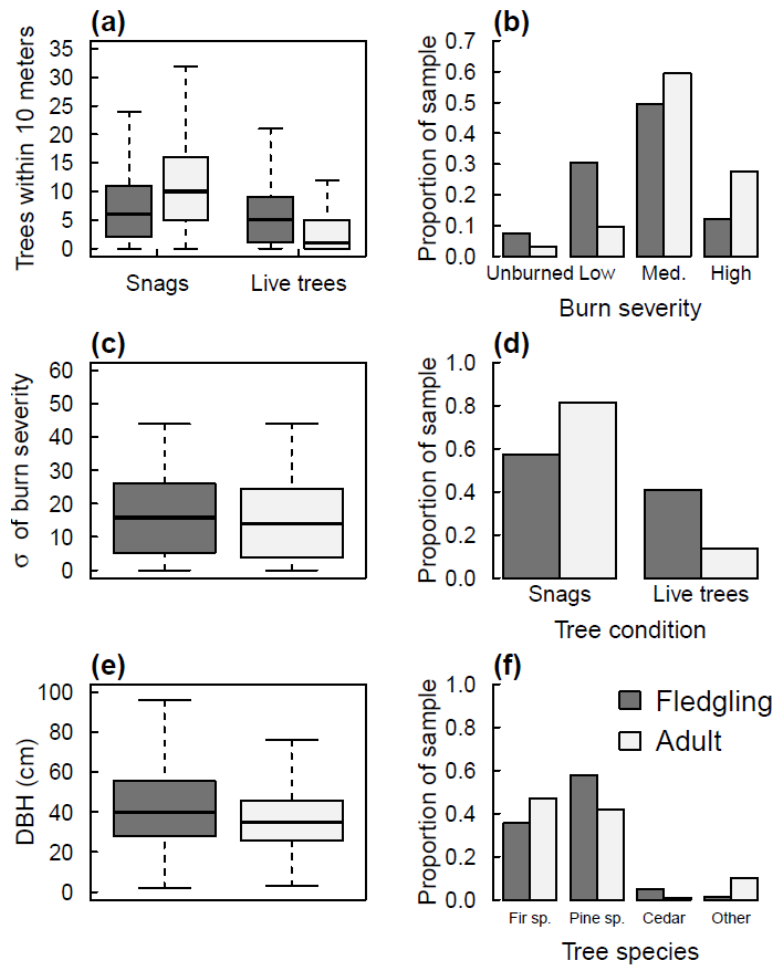


Figure 2. Summary of habitat used by adult and fledgling black-backed woodpeckers in post-fire forests, pooled across all individuals per age group. Plots show (a – c) stand-level measurements and (d – f) tree-level measurements. All comparisons showed significant differences between fledgling and adult habitat use ($p < 0.01$).

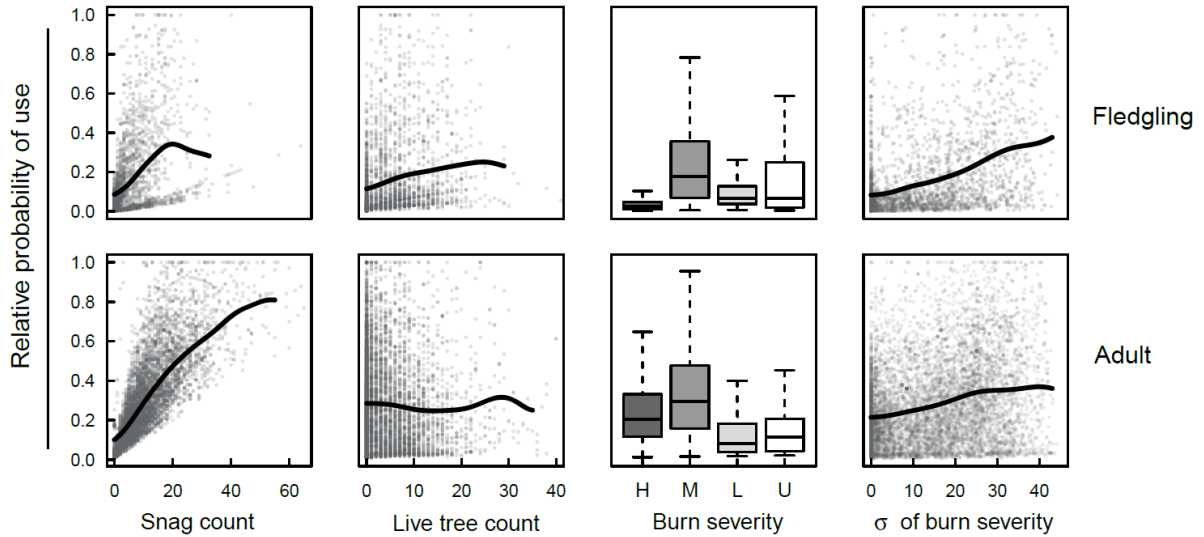


Figure 3. Fitted values from the stand-level resource selection function, ordered across the range of a single covariate of interest. Scatterplot dots show the relative probability of use for each point in the dataset, standardized between 0 and 1 by dividing by the maximum fitted value for each individual. Black lines show a non-parametric regression function through the mean. Note that this plot does not depict the coefficient relationship while holding all other variables constant. Rather, it plots the same set of fitted values based on the covariates of the model and orders them according to the change in a single covariate (Avgar et al., 2017).

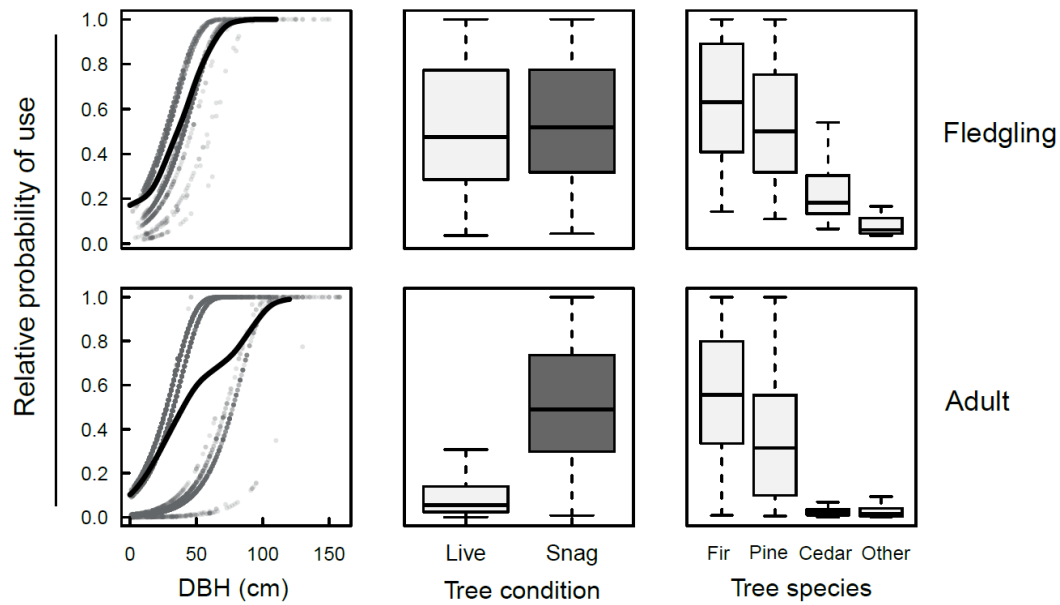


Figure 4. Fitted values from the tree-level resource selection function, ordered across the range of a single covariate of interest. Scatterplot dots show the relative probability of use for each point in the dataset, standardized between 0 and 1 by dividing by the maximum fitted value for each individual. Black lines show a non-parametric regression function through the mean. Note that this plot does not depict the coefficient relationship while holding all other variables constant. Rather, it plots the same set of fitted values based on the covariates of the model and orders them according to the change in a single covariate (Avgar et al., 2017).

Supporting Information

Supplement to:

Stillman, A. N., Siegel, R. B., Wilkerson, R. L., Johnson, M., & Tingley, M. W. (2019). Age-dependent habitat relationships of a burned forest specialist emphasize the role of pyrodiversity in fire management. *Journal of Applied Ecology*, **56**, 880–890.

Corresponding author:

Andrew N. Stillman
Department of Ecology & Evolutionary Biology
University of Connecticut
75 N Eagleville Rd U-4043
Storrs, CT 06105 USA
andrew.stillman@uconn.edu

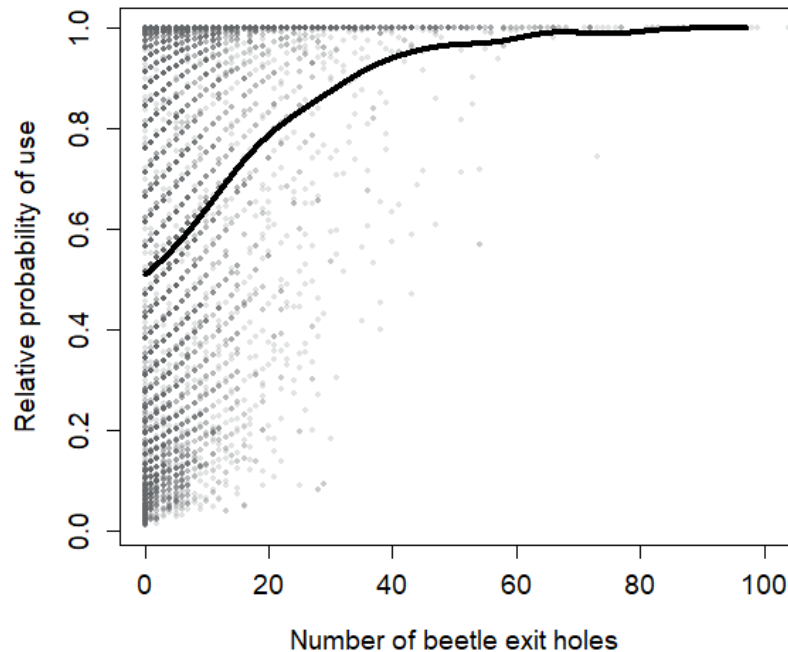


Figure S1. To test for the underlying relationship between number of wood-boring beetle exit holes and the probability of woodpecker use, we built a resource selection function using a subset of adult woodpeckers ($n=41$) where we fully counted the number of exit holes on the trunk between 0–1 m above the ground as an index of past beetle activity on used and available trees. We modeled the probability of snag use as a function of DBH, percent of bark remaining, and the (fully counted) number of beetle holes. Here, we show the fitted values from this model, ordered by the number of beetle holes on each snag. Scatterplot dots show the relative probability of use for each snag in the dataset, standardized between 0 and 1 by dividing by the maximum fitted value for each individual. The black line is a non-parametric regression function through the mean, demonstrating a log-linear shape to the relationship.

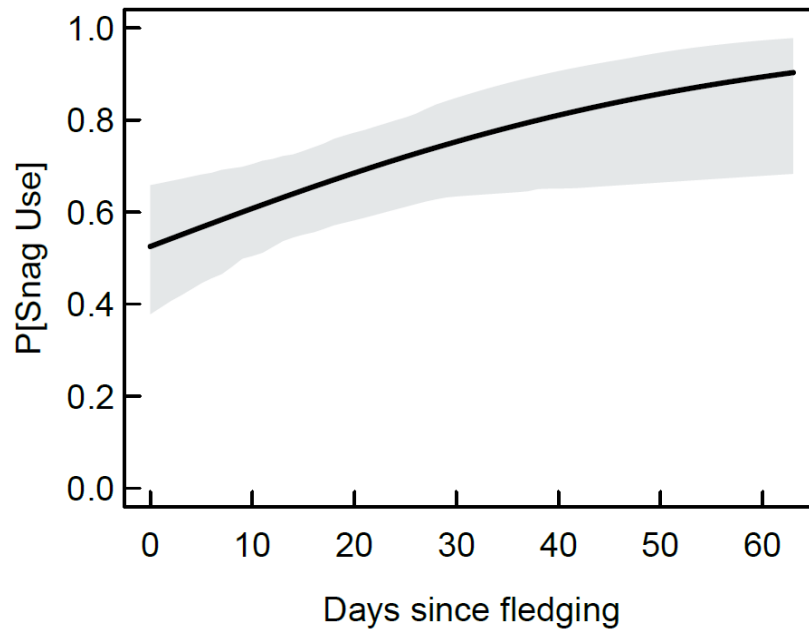


Figure S2. Predicted probability of a fledgling black-backed woodpecker using a snag versus a live tree with increasing time since fledging (line = mean, gray = 95% confidence interval).

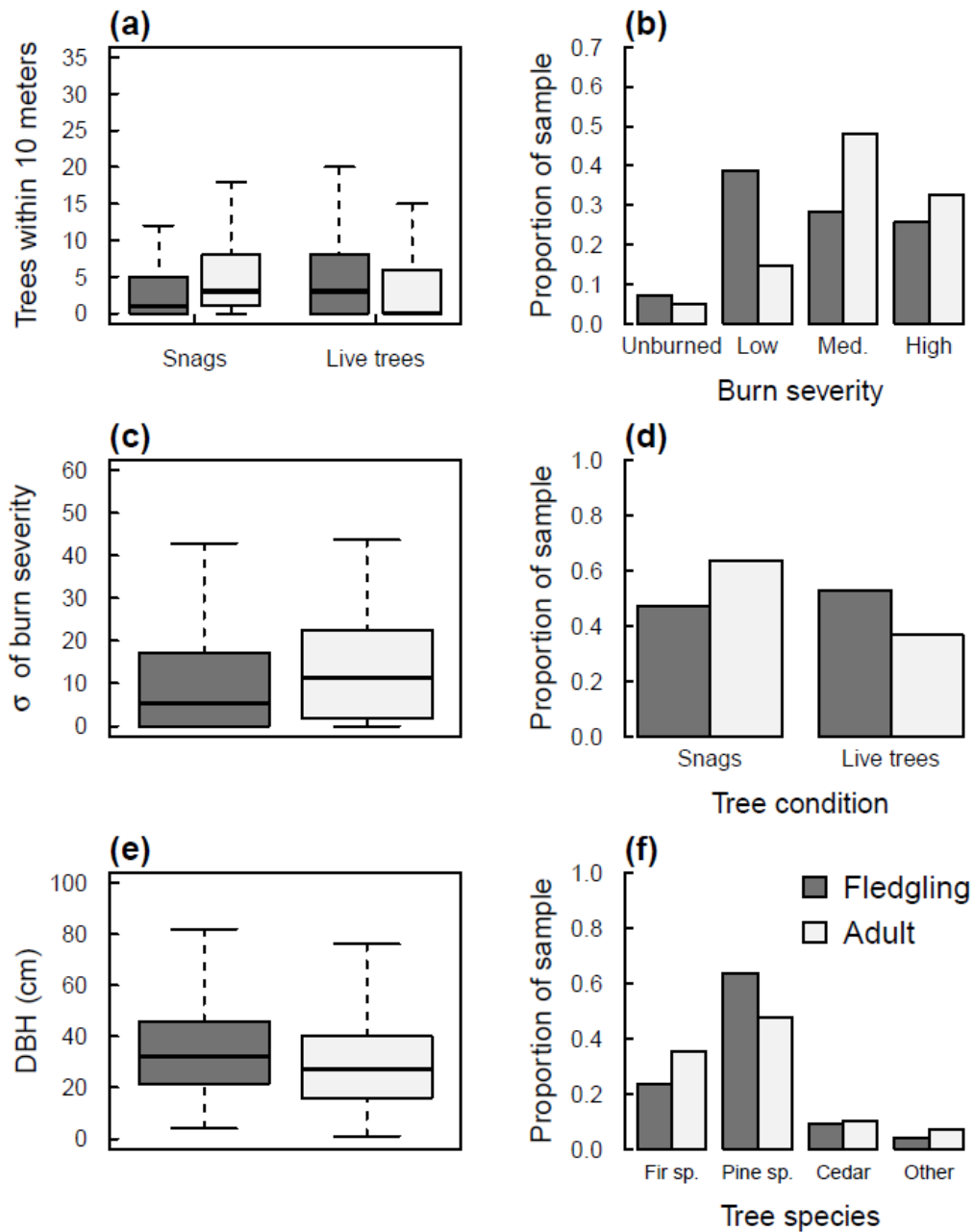


Figure S3. Summary of habitat variables from systematic grid points sampled across the minimum convex polygon bounding black-backed woodpecker tracking points. (a – c) show stand-level measurements and (d – f) show tree-level measurements. Grid points sampled the habitat available to tagged individuals, and differences between fledglings and adults provides evidence that fledgling home ranges incorporated different habitat than adults. Resource selection functions used in this study examine the probability of selecting a given resource type, relative to availability of that resource type across the individual's home range.

Chapter 3:
**Juvenile survival of a burned forest specialist in response to variation in
fire characteristics**

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Stillman, A. N., Siegel, R. B., Wilkerson, R. L., Johnson, M., & Tingley, M. W. (2021). Juvenile survival of a burned forest specialist in response to variation in fire characteristics. *Journal of Animal Ecology*.

ABSTRACT

1. Pyrodiversity, defined as variation in fire history and characteristics, has been shown to catalyze post-fire biodiversity in a variety of systems. However, the demographic and behavioral mechanisms driving the responses of individual species to pyrodiversity remain largely unexplored.
2. We used a model post-fire specialist, the black-backed woodpecker (*Picoides arcticus*), to examine the relationship between fire characteristics and juvenile survival while controlling for confounding factors.
3. We radio-tracked fledgling black-backed woodpeckers in burned forests of California and Washington, USA, and derived information on habitat characteristics using ground surveys and satellite data. We used hierarchical Bayesian mixed-effects models to determine the factors that influence both fledgling and annual juvenile survival, and we tested for effects of fledgling age on movement rates.
4. Burn severity strongly affected fledgling survival, with lower survival in patches created by high-severity fire compared to patches burned at medium to low severity or left unburned. Time since leaving the nest was also a strong predictor of fledgling survival, annual juvenile survival, and fledgling movement rates.
5. Our results support the role of habitat complementation in generating species-specific benefits from variation in spatial fire characteristics – one axis of pyrodiversity – and highlight the importance of this variation under shifting fire regimes. High-severity fire provides foraging and nesting sites that support the needs of adult black-backed woodpeckers, but fledgling survival is greater in areas burned at lower severity. By linking breeding and foraging habitat with neighboring areas of reduced predation risk,

pyrodiversity may enhance the survival and persistence of animals that thrive in post-fire habitat.

INTRODUCTION

A prevailing theory in ecology suggests that spatial variation in environmental features leads to greater biodiversity (Stein et al., 2014). Environmental disturbance from wildfire is a key driver of spatial variation in landscapes worldwide (Bond & Keeley, 2005), and variation in fire regime characteristics – termed pyrodiversity – can have profound impacts on the structure and function of ecological communities (He et al., 2019). Pyrodiversity can occur along multiple axes of variation including fire severity, seasonality, patch size, and time since fire (Bowman et al., 2016; Martin & Sapsis, 1992), and the belief that pyrodiversity can promote biodiversity has become an influential principle guiding the management of fire-prone landscapes (Kelly & Brotons, 2017). Past studies have demonstrated strong positive relationships between pyrodiversity and biodiversity in a variety of ecosystems and taxa (Beale et al., 2018; Ponisio et al., 2016; Tingley et al., 2016), although the magnitude of these relationships depend heavily on regional context (Kelly et al., 2017; Parr & Andersen, 2006).

Pyrodiversity-biodiversity relationships are generally predicated on the idea that heterogeneity in the composition and configuration of burned habitat enhances the coexistence of multiple species, each with a specific niche in the fire regime (Beale et al., 2018; Steel et al., 2019; Tingley et al., 2016). However, the capacity for individual species to benefit from pyrodiversity and the potential mechanisms driving these benefits remain largely unexplored. One hypothesis behind the benefits of pyrodiversity for individual species is that spatial variation in post-fire characteristics may enhance a species' persistence through habitat complementation,

where multiple fire characteristics are needed for an individual to meet resource requirements (Kelly et al., 2017). Accordingly, the spatial configuration of fire characteristics may influence immediate survival through species interactions like competition and predation.

Variation in burn severity within a fire – an important component of pyrodiversity – provides an opportunity to evaluate species-specific effects of fire characteristics on animals that inhabit post-fire landscapes. The black-backed woodpecker (*Picoides arcticus*) is a post-fire specialist closely tied to coniferous forest burned by stand-replacing fire in the western U.S. (Hutto, 2008; Tremblay et al., 2016). Black-backed woodpecker populations thrive where dense stands of snags (standing dead wood) that burned at high severity provide food and nesting resources (Rota et al., 2015; Stillman et al., 2019a). Woodboring beetles (e.g., Cerambycidae, Buprestidae) rapidly colonize burned patches to reproduce in fire-killed snags, and beetle larvae supply a key food source (Murphy & Lehnhausen, 1998). In the western U.S., local black-backed woodpecker populations follow a “boom and decline” cycle in the first 10 years following fire (Tingley et al., 2018), likely reflecting an initial pulse of post-fire colonization followed by gradual population declines perhaps due to decreasing prey abundance (Ray et al., 2019) and decreased recruitment (Siegel et al., 2016). Although breeding black-backed woodpeckers are closely associated with high-severity burns, recent evidence has demonstrated the importance of pyrodiversity for this species (Stillman et al., 2019b). In large fires of northern California, fledging black-backed woodpeckers demonstrate strong selection for areas burned at low and medium severity with higher proportions of live trees (Fig. 1). The severely burned “snag forests” frequented by adults are open, exposed environments that provide high prey densities but little protection from aerial predators. Young fledglings may adjust to this predation-starvation trade-off by moving into areas with greater cover while they are still being provisioned

by parents that largely forage in nearby areas burned at higher severity (Houston et al., 1993; Stillman et al., 2019b). This behavior suggests that fledgling survival may be lower in severely burned patches, and differences between adult and juvenile habitat may be an overlooked mechanism driving species-specific benefits of pyrodiversity.

The post-fledging period in birds is a critical life stage characterized by high juvenile mortality. Across avian taxa, outcomes of this vulnerable period impose marked effects on recruitment, population persistence, and geographic distributions (Cox et al., 2014; Jenkins et al., 2016). Past studies on a variety of species have demonstrated a tendency for fledgling birds to seek areas with high cover after leaving the nest, likely as a strategy to avoid detection by predators (Gow & Wiebe, 2014; King et al., 2006). Predation is particularly high immediately after fledging, a pattern which is generally attributed to limited mobility and weak musculature (Kershner et al., 2004; Naef-Daenzer et al., 2001). In post-fire landscapes, greater variation in burn severity leads to the juxtaposition of high-cover habitats (i.e., live trees in low-severity burn) and high-severity, low-cover patches (Fig. 1). For black-backed woodpeckers that use both these habitats during different life stages, determining how habitat selection decisions govern survival during the vulnerable fledgling stage is important to understanding the species' life history, ecology, and conservation.

We used radio-telemetry to track the survival and movements of juvenile black-backed woodpeckers in burned forests. First, we investigated fledgling survival relationships during the period when fledglings are dependent on provisioning from parents (up to 35 days post-fledging). The contrasting habitat use patterns of adults and fledglings lends support to the hypothesis that spatial variation in burn severity benefits black-backed woodpeckers through habitat complementation, with adults and fledglings using adjacent habitats burned at different

severities (Fig. 1). Thus, we predicted that fledgling survival would be lower in high-severity patches, but also higher in areas with greater variation in burn severity. We additionally predicted that fledgling survival would be higher in more recent burns (< 5 years post-fire) due to increased food availability (Ray et al., 2019). Second, we examined the relationship between fledgling age and movement rates, both of which are predicted to decrease predation risk and increase survival probability (Kershner et al., 2004). Last, we estimated annual survival for juvenile black-backed woodpeckers and tested whether this demographic parameter is a potential mechanism behind observed population declines with time since fire (Tingley et al., 2018).

METHODS

Study sites

We collected survival and movement data from black-backed woodpeckers in seven distinct burned areas in two U.S. states, Washington and California (Fig. 2). In northern California (Plumas, Lassen, and Shasta counties), we tracked woodpeckers in the Moonlight (burned in 2007), Chips (2012), and Bald (2014) wildfires (Table 1). The Moonlight and Chips fires burned predominantly Sierran mixed conifer forest with a history of mixed-severity wildfire, and the Bald fire burned an area dominated by eastside pine forest with a historical regime of frequent, low- to mixed-severity wildfire (Agee, 1998). We also collected data from four fires in Yakima county, Washington: Kaboom (prescribed burn: 2009), Angel 1 (prescribed burn: 2014), Meeks (wildfire: 2015), and Angel 2 (prescribed burn: 2016; Table 1). These fires burned primarily Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) forest types characterized by a mixed-severity fire regime (Agee, 1998; Reilly et al., 2017). Although the Washington fires were considerably smaller than the California fires, they each

included patches of stand-replacing fire >10 ha (Table 1), indicating approximately equal access to a diversity of post-fire habitats for individual woodpeckers. Post-fire logging occurred in some areas of the California fires, ranging from selective thinning and roadside salvage to clear-cut logging on private lands.

Woodpecker capture and tracking

We used radio-telemetry to monitor survival and track the movements of black-backed woodpecker fledglings. During the spring and summer of 2016–2018, we captured nestlings just prior to expected fledging (mean = 1.6 days before fledging) using the hole-saw method to access nest contents (Ibarzabal & Tremblay, 2006). We conducted standard measurements on each nestling and fit birds with 1.6-g connectivity tags (Model CTx Ag 392, Lotek Wireless Inc. Newmarket, Ontario, Canada) using an adjustable leg-loop harness with elastic beading cord (Rappole & Tipton, 1991). A programmable on/off calendar schedule on these transmitters allowed us to extend battery life over a year post-deployment (signal transmitted May–August, September–November, and April–June). In 2016, we additionally fit a subset of individuals with non-programable 1.6-g transmitters (Model BD-2, Holohil Systems, Carp, Ontario, Canada) attached to the dorsal surface of an inner rectrix feather with monofilament and a thin layer of ethyl cyanoacrylate. We marked all nestlings with a unique combination of color bands and a numbered USGS leg band before returning them to their nest cavity. We ensured that transmitters weighed less than 3% of average body mass to minimize transmitter impact on behavior and survival (Fair et al., 2010). Prior to deployment, we coated transmitters in a thin layer of quick-dry epoxy as added protection against transmitter failure during predation events.

After a nest successfully fledged (mean fledge date = June 16th), we tracked tagged fledglings on foot approximately every 3–5 days until early August. Once located, observers

recorded whether the bird was alive or dead and attempted to follow individuals for 30–60 minutes. We recorded location coordinates at each tree that a fledgling used during a tracking bout and assigned the burn severity within 50 m to one of four potential burn severity categories based on tree canopy mortality (unburned: 0%, low: >25%, medium: 26–80%, high: >80%). Although we only tagged birds from nests within fire boundaries, fledglings moved freely across burn perimeters and sometimes used the surrounding unburned forest. We considered each tracking bout as a single survival observation (alive or dead) and used repeated locations within a bout to assess habitat use.

We recorded an individual as dead if remains were found with a transmitter or if the transmitter was found with evidence of predation (e.g., blood on harness, beak indentations on coating), and we completed necropsies on two birds found with full-body remains (Washington Animal Disease Diagnostic Laboratory, College of Veterinary Medicine, Washington State University). Seven individuals went missing within six days of fledging, and we were unable to locate these birds despite tracking their siblings, searching over an extensive area, and observing their parents as they provisioned young. We assumed that these seven individuals died and their transmitters were either destroyed or carried outside of the study area, and we included these assumed mortality events in subsequent analyses.

After August 1st each year, we transitioned to a more intermittent tracking schedule with the goal of locating each bird at least 3–5 times between August and November. We found that many birds dispersed from natal breeding grounds during this time period, and we employed two strategies to locate dispersing individuals. First, we drove road networks near natal territories with handheld and vehicle-mounted antennas. Second, we conducted aerial telemetry flights with fixed-wing aircraft. These flights included a series of concentric circles around previous

locations and systematic search transects with 5-km spacing. We concentrated flight effort within 35 km of natal sites, but specific searches sometimes extended >60 km away from a bird's last-known location. If a transmitter signal was located from the air, we recorded location coordinates and visited the area on foot to determine if the bird was alive or dead. Programmable transmitters switched off during the winter and turned back on the following spring, allowing use of on-the-ground surveys and aerial telemetry for tagged birds up to one year after fledging. Of 34 birds that survived to August 1st, we located 21 in the fall and 14 the following spring. Birds that were lost >6 days after fledging were censored after their last location, and not assumed deceased (see modeling details, below).

Survival covariates

We assessed spatial fire characteristics using 30 x 30m rasters of categorical burn severity from Monitoring Trends in Burn Severity (MTBS; <https://www.mtbs.gov/>). Burn severity was defined using the relativized difference in normalized burn ratio (RdNBR; Miller & Thode 2007), a standard measure of fire effects on vegetation, and classified as unburned, low, medium, or high burn severity. The three prescribed fires in our study area (Kaboom, Angel I, and Angel 2) did not meet thresholds for inclusion in the MTBS dataset, so we calculated RdNBR using regional composites of the normalized burn ratio for the year before and after each fire (Miller & Thode, 2007; Reilly et al., 2017). Within prescribed fires, we validated RdNBR thresholds for burn severity classes by calculating RdNBR values for the nearby Meeks wildfire, applying the classification thresholds, and comparing these to the Meeks MTBS data using a spatial sample of 1000 random points. This confirmed that our RdNBR and classified burn severity layers produced results that were correctly scaled and tightly correlated with MTBS (Pearson's correlation: RdNBR $r = 0.83$, classified $r = 0.76$).

We calculated an index of fine-scale variation in burn severity – a component of pyrodiversity – for each tracking bout using the inverse Simpson’s index of diversity ($1/D$) for all classified burn severity pixels within a 100-m buffer of tracking points (Ponisio et al., 2016). In this case, the inverse Simpson’s index ranges from 1 (all pixels equal) to 4 (pixels equally distributed between 4 different severity classes). This metric conveys information about the representation and evenness of severity classes, providing a single metric of variation that may be useful to land managers. In addition, we used field-collected data to assign a binary variable to each tracking bout indicating whether or not a fledgling spent >50% of observation time in high severity burn. For points where field-based burn severity was lacking ($n = 152$ of 2,735), we extracted the value from the classified burn severity raster. While 50% of observation time in high-severity burn represents an arbitrarily conservative threshold, we explored model sensitivity to this cut-off and found that results did not qualitatively change based on threshold levels, even with thresholds as low as 25% (Table S1).

Because nestlings were weighed at a range of days prior to fledging, we standardized raw mass values by subtracting the mean mass of birds banded 0–2 days before fledging and 3+ days before fledging separately. Mass of nestlings at capture was variable, with a slight increase in average mass 2 days before fledging (Fig. S1).

Survival analysis

We examined fledgling survival relationships using logistic exposure models fit within a Bayesian framework (Schmidt et al., 2010). We developed two separate models based on our quantities of interest: (1) the probability of surviving to “independence,” which occurs approximately 35 days after fledging (Stillman et al., 2019b), and (2) the probability of surviving approximately 9 months, to the beginning of the next breeding season. We assumed that the

survival of individual i over interval j followed a Bernoulli distribution $y_{ij} = \text{Bernoulli}(\theta_{ij})$ where $y_{ij} = 1$ if individual i survived interval j , $y_{ij} = 0$ if the individual died, and θ_{ij} is the probability of individual i surviving interval j . Here, θ represents the daily survival probability, s , raised to the length of the risk exposure period such that $\theta_{ij} = s^{t_{ij}}$, where t_{ij} is the length of interval j for individual i . We modeled s_{ij} using a logit-link function $\text{logit}(s_{ij}) = \beta X$, where β represents a vector of intercept and slope coefficients and X represents a matrix of covariates. In this way, the model allows for uneven sampling intervals and the inclusion of interval-specific covariates such as habitat use. We included a nest-level identifier as a random intercept in each model to account for repeated observations of individuals from the same nest, which generally shared similar covariate values (e.g. same fledging date for siblings). All survival models used a $\text{Normal}(\mu = 4.00, \tau = 0.25)$ prior distribution on the overall intercept coefficient, which centers the prior on a reasonable value for daily survival rate. We used agnostic priors with slight regularization, $\text{Normal}(\mu = 0, \tau = 0.25)$, on all fixed effects and a uniform prior (0.1, 3) on the random effect standard deviation.

For our model of 35-day fledgling survival ($n = 439$ visit intervals), we developed a set of candidate models based on *a priori* hypotheses about survival relationships (Table 2). We started with a single model that included only the covariates for which we had strong, directional predictions for their effects on survival: high severity burn, diversity in burn severity classes, years since fire, and days since fledging. Next, we iteratively tested this model with the addition of one of the following covariates: ordinal fledging date, study region (California or Washington), sex, and mass. These four variables all have associations with survival supported in the literature (Cox et al., 2014; Kilgo & Vukovich, 2012; Naef-Daenzer et al., 2001), but were not the main focus of our study and therefore we considered them as potential nuisance variables.

Model comparisons also included a full model with all eight predictors. We compared models using leave-one-out cross validation (LOO) to estimate the pointwise out-of-sample prediction accuracy (Vehtari et al., 2018). We also performed model comparisons using the widely applicable information criterion (WAIC; Watanabe 2010) and confirmed that results were similar (Table S2). We made inference using the best supported model based on ΔLOOIC (Arnold, 2010).

We used covariates from the top 35-day survival model to parameterize a model of annual juvenile survival that included all tracking bouts from the first year after birds were tagged ($n = 638$ visit intervals). This model did not include habitat characteristics as predictors because birds often moved extensively during the long intervals between consecutive visits. Although some birds likely dispersed beyond the boundaries of our aerial telemetry searches, our censorship criteria meant that daily survival estimates were only informed by detected transmitters and that mortality was not confounded by emigration. We calculated annual juvenile survival by summarizing the posterior distribution of cumulative survival probability for the first 350 days after fledging, which represents the time period between the average ordinal nest fledging date (June 16th) and June 1st of the following year, when most pairs have initiated nesting.

Analysis of movement rates

We calculated a metric of fledgling mobility, km moved per hr, for all tracking bouts that lasted longer than 25 min during the first 35 days post-fledging. Using the R package ‘adehabitatLT’ (Calenge, 2006), we summed the straight-line distances between all consecutive trees where we observed an individual during a tracking bout, divided this distance by the total minutes of observation time, and multiplied by 60 to obtain the distance traveled per hour of

observation. We modeled movement rate as a function of days since fledging using a Bayesian lognormal regression. We used vague prior distributions, $N(\mu = 0, \tau = 0.01)$, on fixed effects, and we included a nest-level random effect with a vague prior distributed as $\Gamma(r = 0.001, \lambda = 0.001)$.

Bayesian inference

We fit all models in R version 3.6.3 using JAGS and the package ‘R2jags’ (R Core Team, 2020; Su & Yajima, 2015). Each model ran 3 chains of 20,000 iterations with a burn-in of 5,000 and a thin rate of 10, giving a final posterior sample of 4,500. We confirmed that the Gelman-Rubin statistic was <1.1 for every estimate and visually inspected traceplots to assess convergence (Youngflesh, 2018). All continuous variables were centered and standardized prior to modeling, and we made inference using 95% Bayesian credible intervals. To evaluate model fit, we conducted posterior predictive checks with Bayesian p-values (Gelman et al., 1996) for test statistics representing apparent survival rates and the mean and standard deviation of log-transformed movement rates.

RESULTS

We tracked the survival of 84 fledgling blacked-backed woodpeckers from 39 nests in seven different post-fire areas. Nests generally contained 2–3 young (mean = 2.5), and parents tended to split the brood after nests fledged, with each parent separately provisioning 1–2 offspring. In total, we collected tracking data at 2,735 points during 722 tracking bouts, with an average of 8.6 bouts per bird. Of 439 tracking bouts on dependent fledglings, 53 of 220 were assigned to high-severity burn ($>50\%$ of observation time in high severity) in California, and 35 of 219 were assigned to high-severity burn in Washington. Apparent survival to independence

35-days after fledging was 44% (47 deaths; Table 1) with seven additional deaths recorded 35–350 days post-fledging.

Most deaths could be attributed to predation by hawks or owls, and we frequently found transmitters surrounded by body remains or plucked feathers. Two transmitters were recovered below northern goshawk (*Accipiter gentilis*) nests and one transmitter each was located in – or next to – the nests of a red-tailed hawk (*Buteo jamaicensis*), western screech owl (*Megascops kennicottii*), and Cooper’s hawk (*Accipiter cooperii*). Of five deaths with full body remains, three were found in exposed habitat within high-severity burns directly after unusually severe weather (e.g., early summer thunderstorms). A necropsy on another fledgling revealed the presence of tapeworms, and a necropsy on a final bird detected the presence of pneumonia, although bodily damage suggested that predation may have been the proximate cause of death.

We made inference using the best supported model for fledgling survival to independence, which included fixed effects of burn severity, diversity in burn severity, years since fire, days since fledging, and ordinal fledging date (Table 2). Daily fledgling survival probability showed a strong relationship to burn severity, with lower survival in areas with high burn severity compared to unburned, low-, and medium-severity burn (Fig. 3a; Table 3). The cumulative probability of a fledgling surviving 35 days in unburned to medium-severity burned forest was 0.53 (95% CrI = 0.37–0.70), but survival decreased to 0.13 (95% CrI = 0.02–0.33) for birds using only high-severity patches. Controlling for burn severity, years since fire and diversity in burn severity did not show strong relationships, but predicted values showed a slight increase in survival with increasing diversity in burn severity and a weak decrease in survival in older fires. Fledgling survival was strongly related to the number of days since fledging, with lower survival in younger individuals. The ordinal date that a nest fledged showed a weak,

negative relationship, indicating a tendency for earlier nests to produce fledglings with higher survival (Fig. 3; Table 3).

We found a strong positive relationship between fledgling movement rate and the number of days since fledging ($\beta = 0.82$, 95% CrI = 0.57–1.07; Fig. 4). Immediately after leaving the nest, many fledglings traveled to forest patches with live trees where they moved infrequently and received provisioning from adults. As fledglings grew older, activity increased and fledglings moved between trees more often. As they neared independence, we observed fledglings accompanying foraging adults and attempting to forage independently in low- and high-severity burn patches.

Survival rates generally remained high once fledglings reached independence. In all habitats combined, a juvenile woodpecker had a cumulative survival probability of 0.23 (0.05, 0.45) from fledging to the first breeding attempt the following spring. The number of days since a juvenile left the nest was the strongest predictor of survival probability, with mean daily survival rates rising from an average of 0.972 (0.954, 0.985) during the dependent fledgling period to 0.998 (0.996, 0.9997) after independence (Table 4). Once surviving to independence, the cumulative probability of additionally surviving to June 1st the following spring was 0.60 (0.25, 0.92).

Model evaluation

Both the 35-day and annual survival models closely approximated the apparent interval survival rate for fledgling black-backed woodpeckers and showed no evidence for lack of model fit (35-day survival $p_b = 0.21$, annual survival $p_b = 0.38$). Posterior predictive tests also indicated no significant lack of fit for our model of fledging movement rates based on the mean and standard deviation of observed data (p_b for the mean = 0.49, p_b for standard deviation = 0.48).

DISCUSSION

Spatial variation in fire characteristics can structure not only the biotic community arising after fire, but also the populations of individual species using burned areas (He et al., 2019; Kelly & Brotons, 2017). Here, we demonstrate that spatial fire characteristics interact with fledgling survival rates in a post-fire specialist. Despite the importance of high-severity patches for black-backed woodpecker foraging and reproduction in our study region (Hutto, 2008), survival to independence was four times higher for fledglings that avoided high-severity patches compared to fledglings that primarily used high-severity burn, even when controlling for effects of fledgling age, mass, sex, fledging date, and years since fire. This result supports the hypothesis that fledgling habitat selection confers fitness benefits consistent with the predation-starvation hypothesis: while fledglings are provisioned by adults, they can avoid exposed areas with increased predation risk (Houston et al., 1993; Stillman et al., 2019b).

Predicted fledgling survival to independence was notably low for fledglings that primarily used high-severity burned patches (mean = 13% survival), but we caution that the majority of fledglings used a mix of burn severities during their first 35 days after leaving the nest. Still, 16 birds in our sample used >50% high-severity habitat during every tracking bout, and of these, 15 of 16 (94%) did not survive to independence. In addition, subtle differences in forest type, management history, and fire size between Washington and California could represent sources of variation in our dataset. However, the survival model that included an effect of region (i.e., U.S. state) received little support, indicating that underlying survival relationships were similar across sampling sites.

Of the non-habitat covariates that we examined, the number of days since fledging had the strongest effect on fledgling survival. We also found that movement rates increased substantially as fledglings grew older, likely reflecting post-fledging muscle development and the gradual shift toward independent foraging during the first 35 days out of the nest. New fledglings experience high predation rates in many bird species, especially when fledglings are weak fliers or engage in vocal begging behaviors (Fisher & Davis, 2011; Kershner et al., 2004). In our study, 53% of deaths occurred within the first three days after fledging. We hypothesize that the strong positive relationship between fledgling age and survival in our study corresponds to an increase in mobility and predator evasion as fledglings grow older. In the field, we observed gradual decreases in fledgling “begging” behaviors and increases in independent foraging during the first 35-days after fledging.

The day of year that nestlings fledged had a weak, negative effect on fledgling survival, with slightly higher survival in early-season fledglings. This relationship may stem from seasonal effects, such as changes in predation and food availability, or the quality of breeding adults (Naef-Daenzer et al., 2001; Perrins, 1970). Previous work on black-backed woodpeckers has shown a strong negative day-of-year effect on nest survival (Stillman et al., 2019a), which suggests that a similar mechanism may affect both vital rates with carry-over effects from one life stage to another. Within the burned forests that we studied, it is possible that more experienced breeders nest earlier in the breeding season and have higher offspring survival compared to less-experienced conspecifics (Perrins, 1970).

We did not find evidence for a strong relationship between juvenile survival and years since fire, although parameter estimates of this effect were negative for both 35-day and annual survival models. These results suggest that juvenile survival is not the principal demographic

mechanism driving the observed decline of local populations within burned areas during the first decade following fire (Rota et al., 2014; Tingley et al., 2018). Juvenile recruitment may influence local population size through variation in the probability of long-distance dispersal rather than survival (Siegel et al., 2016), although this hypothesis has not been empirically tested. In addition to influencing black-backed woodpecker population density, the number of years since fire also has a marked effect on the structure of forests burned at high severity. Snags fall over time (Grayson et al., 2019), food resources may decline (Ray et al., 2019), and high-severity patches become even more open and exposed to aerial predators with increasing years since fire. These successional changes may incrementally increase predation risk for fledglings in high-severity patches over time, although our data do not support this as a strong effect.

More broadly, our results provide evidence to support the role of habitat complementation in generating species-specific benefits of pyrodiversity over the full life cycle of animals (Kelly et al., 2017). Variation in burn severity within post-fire habitat yields high-severity areas that are close to forest patches with live trees (low-severity burn or unburned), which may provide needed habitat structure for multiple life stages in close proximity. This is evidenced in adult black-backed woodpeckers, which select foraging and nesting sites near ecotones between high- and low-severity burn (Stillman et al., 2019a; Stillman et al., 2019b). As the proximate cause of mortality, fledgling predation may exert selective pressure for adults to nest near low-severity or unburned forest, where fledglings with limited flying ability may seek cover rapidly after leaving the nest. Taken together, these habitat selection and survival patterns support the idea that the distribution of species on the burned landscape is driven not only by habitat quality, but also by the presence of higher trophic levels and spatial patterns of predation risk (Creel et al., 2005; Kelly et al., 2017). By linking resource-rich foraging and breeding

habitat with areas of reduced predation risk, variation in burn severity – as well as other aspects of pyrodiversity – may enhance the survival and persistence of animals that specialize on post-fire habitat. Although our study only focused on a single fire-associated species, the expected mechanisms underlying this phenomenon may apply broadly to other animals, particularly prey species, in fire-prone landscapes of western North America.

We note that our study occurred in a region historically dominated by a mixed-severity fire regime, where previous research has shown positive relationships between pyrodiversity and biodiversity (Ponisio et al., 2016; Steel et al., 2019; Tingley et al., 2016). Although other species likely benefit from variation in spatial fire characteristics, we caution that the role of pyrodiversity in animal conservation must be considered at a regional level, where the effects of pyrodiversity are evaluated in the context of a historical fire regime (Kelly & Brotons, 2017; Parr & Andersen, 2006). Fire regimes in the western U.S. show a pattern of increasing fire intensity and larger high-severity patches in recent decades (Steel et al., 2018; Stevens et al., 2017). These changes may lead to overall decreases in pyrodiversity, including important ecotones between low- and high-severity patches (Stevens et al., 2017). In addition to potential community-level effects of increased habitat homogeneity after fire, our research suggests that declining pyrodiversity may also influence individual species through stage-dependent effects of post-fire habitat structure on demographic rates.

DATA AVAILABILITY

Input data and model code in JAGS language are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.0rxwdbrzt> (Stillman et al., 2021).

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Table 1. Fire characteristics and sample size for study sites where we tracked fledgling black-backed woodpeckers.

Region	Fire name	Size (ha)	Percent high severity*	Years since fire during study	Birds tagged (alive, dead)†
Washington	Kaboom	2611	3%	7, 8	14 (6, 8)
Washington	Angel 1	571	4%	2	1 (0, 1)
Washington	Meeks	552	6%	2, 3	13 (4, 9)
Washington	Angel 2	453	11%	1	9 (5, 4)
California	Moonlight	26 509	44%	9, 10	14 (7, 7)
California	Chips	31 114	21%	5, 6	19 (6, 13)
California	Bald	16 258	16%	3, 4	14 (9 , 5)

* Percent of total fire area that burned at high severity (data from MTBS).

† Numbers reflect the known fates of tagged birds during the first 35 days after fledging.

1 Table 2. Model selection results for 6 *a priori* candidate models of 35-day fledgling survival for
2 black-backed woodpeckers in burned forests of Washington and California, USA. We employed
3 leave-one-out cross-validation to compare Bayesian models using the information criterion
4 LOOIC, presented here on the deviance scale. Models are shown in order of increasing LOOIC
5 (lower value = better relative fit).

Model	LOOIC	ΔLOOIC
High severity + Diversity in burn severity + Years since fire + Days since fledging + Ordinal fledging date	307.2	0
High severity + Diversity in burn severity + Years since fire + Days since fledging	308.4	1.2
High severity + Diversity in burn severity + Years since fire + Days since fledging + Region	309.4	2.2
High severity + Diversity in burn severity + Years since fire + Days since fledging + Sex	311.4	4.2
High severity + Diversity in burn severity + Years since fire + Days since fledging + Mass	311.5	4.3
High severity + Diversity in burn severity + Years since fire + Days since fledging + Ordinal fledging date + Region + Sex + Mass	315.4	8.2

6

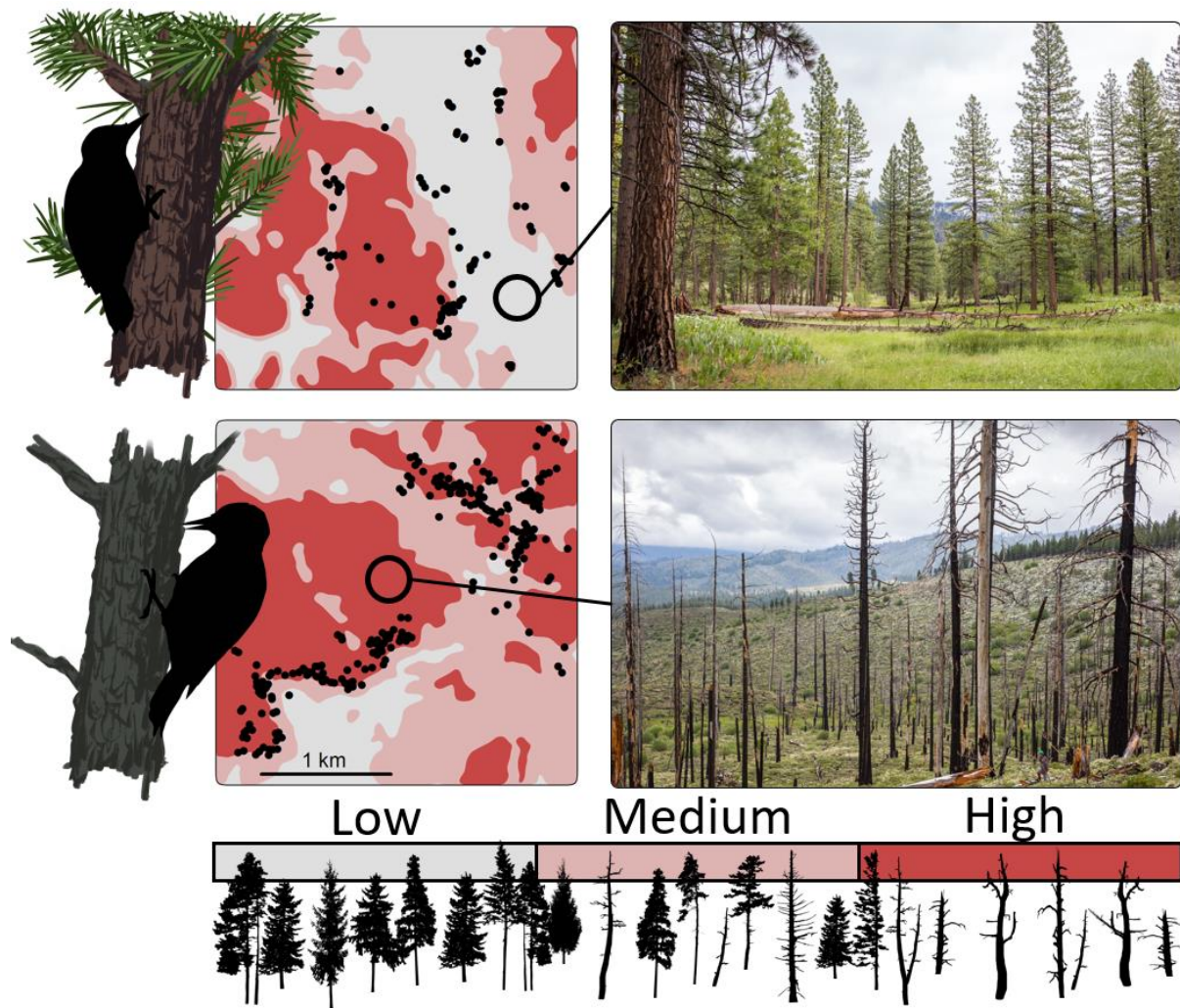
Table 3. Posterior means and 95% credible intervals for estimated parameters from two models of fledgling black-backed woodpecker survival during the first 35 days after leaving the nest. Inference was made using the top model with the lowest LOOIC; the full model including all parameters is shown for reference. Items in bold indicate 95% credible intervals that do not overlap zero.

Covariate	Top model	Full model ($\Delta\text{LOOIC} = 8.2$)
Intercept	3.99 (3.48, 4.57)	3.18 (1.22, 5.35)
High severity	-1.26 (-2.02, -0.54)	-1.27 (-2.04, -0.52)
Diversity in burn severity	0.20 (-0.13, 0.56)	0.21 (-0.15, 0.57)
Years since fire	-0.23 (-0.67, 0.19)	-0.35 (-0.89, 0.17)
Days since fledging	0.97 (0.50, 1.49)	0.97 (0.50, 1.49)
Ordinal fledging date	-0.38 (-0.84, 0.04)	-0.33 (-0.82, 0.13)
Region (California)	—	0.26 (-0.75, 1.26)
Sex (Female)	—	0.30 (-0.50, 1.07)
Mass	—	0.19 (-0.35, 0.75)

13 Table 4. Posterior means and 95% credible intervals from the model of juvenile black-backed
 14 woodpecker annual survival in burned forests of Washington and California, USA.

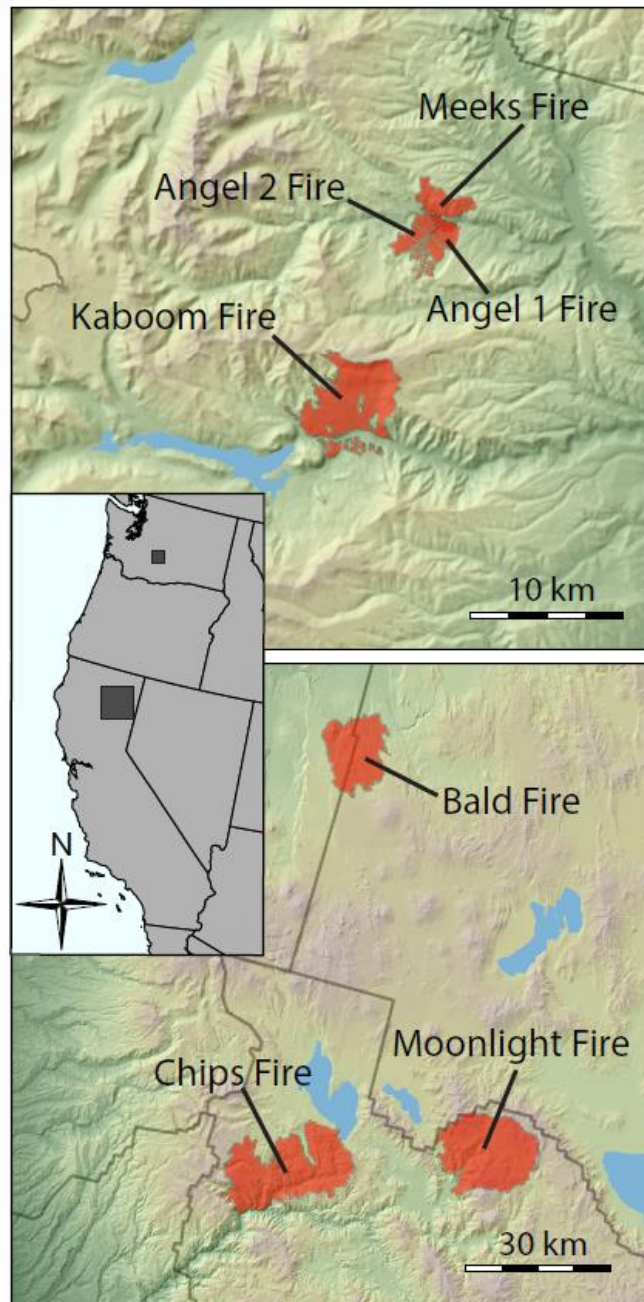
Covariate	Estimate (95% CrI)
Intercept	3.48 (2.92, 4.08)
Years since fire	-0.18 (-0.79, 0.35)
Days since fledging	0.35 (0.17, 0.72)
Ordinal fledging date	-0.37 (-1.00, 0.19)

15



16

17 Figure 1. Conceptual diagram showing patterns of age-dependent habitat selection in fledgling
 18 (top) and adult (bottom) black-backed woodpeckers using burned forests. Fledglings select
 19 habitat that burned at low- to medium-severity, where live trees provide cover from predators,
 20 while adult woodpeckers select habitat that burned at high severity, where dead trees provide
 21 abundant prey. Data from Stillman et al. (2019b).



22

23 Figure 2. Burned areas (red polygons) where we tagged fledgling black-backed woodpeckers in

24 Washington (top) and California (bottom). Gray lines represent county boundaries.

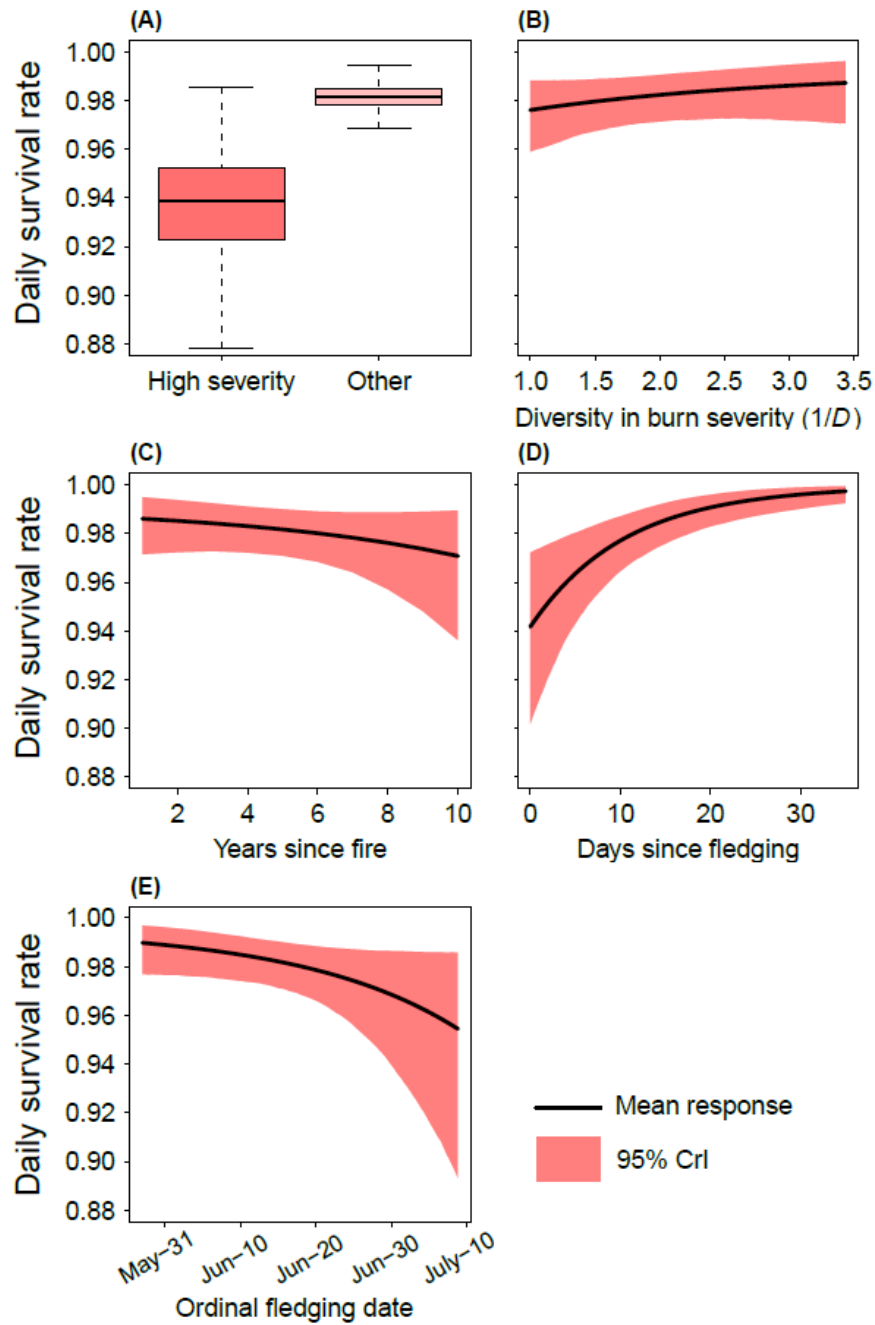


Figure 3. Modeled relationships for daily survival rate of fledgling black-backed woodpeckers during the first 35 days after fledging, when young typically depend on their parents for provisioning. The strongest predictors of survival were burn severity (A) and days since fledging (D).

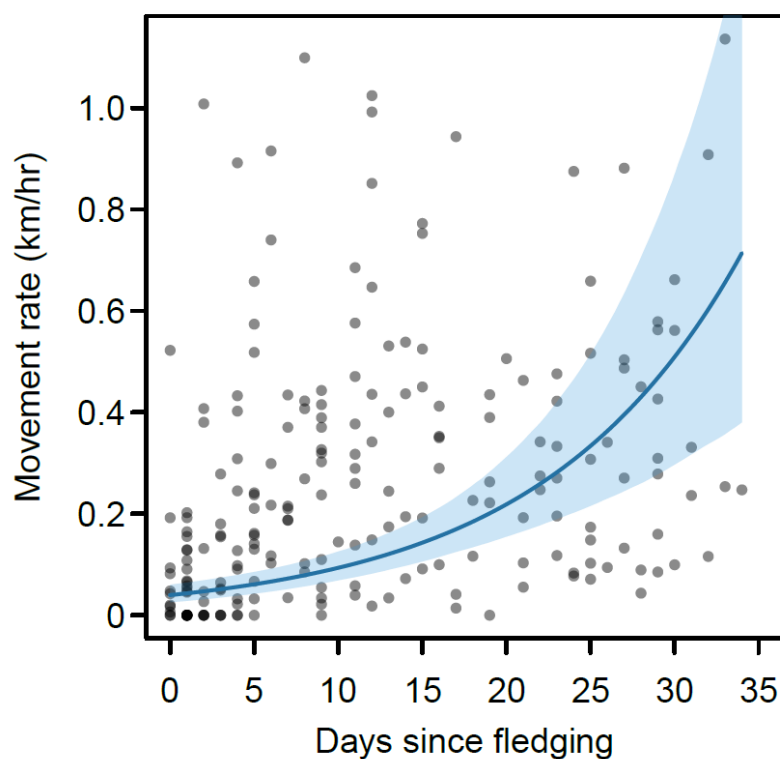


Figure 4. The relationship between the number of days since a fledgling black-backed woodpecker left the nest and movement rate recorded during radio-telemetry tracking bouts. Mean prediction and 95% CrI are shown in blue, and dots represent raw data with transparency added to visualize overlapping points.

Supplemental Material

Supplement to:

Stillman et al. (2021) Juvenile survival of a burned forest specialist in response to variation in fire characteristics. *Journal of Animal Ecology*.

Corresponding author:

Andrew N. Stillman

Ecology & Evolutionary Biology, University of Connecticut, Storrs, CT

Phone: +1 (860) 486-5522

Email: stillman.andrewn@gmail.com

Table S1. We assigned a binary variable to each tracking bout indicating whether or not a fledgling spent a certain percentage of a tracking bout in forest burned at high severity. We used a conservative 50% threshold for our models, but we explored model sensitivity and found that results did not qualitatively change based on threshold levels. Parameter estimates (with 95% CrI) are shown for the top model based on LOOIC and the full model that included all parameters. Items in bold indicate 95% credible intervals that do not overlap zero.

Covariate	50% threshold	40% threshold	25% threshold
<i>Top model of 35-day survival</i>			
Intercept	3.99 (3.48, 4.57)	3.98 (3.47, 4.56)	3.97 (3.46, 4.52)
High severity	-1.26 (-2.02, -0.54)	-1.15 (-1.85, -0.43)	-1.03 (-1.75, -0.33)
Diversity in burn severity	0.20 (-0.13, 0.56)	0.21 (-0.13, 0.57)	0.22 (-0.12, 0.58)
Years since fire	-0.23 (-0.67, 0.19)	-0.21 (-0.67, 0.18)	-0.22 (-0.69, 0.18)
Days since fledging	0.97 (0.50, 1.49)	1.00 (0.53, 1.52)	1.02 (0.55, 1.54)
Ordinal fledging date	-0.38 (-0.84, 0.04)	-0.36 (-0.83, 0.08)	-0.36 (-0.82, 0.07)
<i>Full model of 35-day survival</i>			
Intercept	3.18 (1.22, 5.35)	3.12 (1.27, 5.27)	3.11 (1.17, 5.12)
High severity	-1.27 (-2.04, -0.52)	-1.16 (-1.87, -0.42)	-1.05 (-1.76, -0.33)
Diversity in burn severity	0.21 (-0.15, 0.57)	0.22 (-0.12, 0.58)	0.22 (-0.14, 0.59)
Years since fire	-0.35 (-0.89, 0.17)	-0.34 (-0.86, 0.16)	-0.33 (-0.86, 0.16)
Days since fledging	0.97 (0.50, 1.49)	1.01 (0.54, 1.53)	1.02 (0.54, 1.52)
Ordinal fledging date	-0.33 (-0.82, 0.13)	-0.30 (-0.79, 0.16)	-0.31 (-0.80, 0.14)
Region (California)	0.26 (-0.75, 1.26)	0.27 (-0.71, 1.18)	0.24 (-0.72, 1.19)
Sex (Female)	0.30 (-0.50, 1.07)	0.32 (-0.43, 1.07)	0.34 (-0.41, 1.08)
Mass	0.19 (-0.35, 0.75)	0.20 (-0.35, 0.73)	0.20 (-0.35, 0.75)

Table S2. WAIC (widely applicable information criterion) model selection results for 6 candidate Bayesian models of fledgling black-backed woodpecker 35-day survival in burned forests of Washington and California, USA. WAIC values were calculated using pointwise log-likelihood values from 4,500 posterior draws, and candidate model comparisons resulted in the same top three models as LOOIC model selection.

Model	WAIC	ΔWAIC
High severity + Diversity in burn severity + Years since fire + Days since fledging + Ordinal fledging date	306.0	0
High severity + Diversity in burn severity + Years since fire + Days since fledging	307.0	1.0
High severity + Diversity in burn severity + Years since fire + Days since fledging + Region	307.9	1.9
High severity + Diversity in burn severity + Years since fire + Days since fledging + Mass	310.0	4.0
High severity + Diversity in burn severity + Years since fire + Days since fledging + Sex	310.2	4.2
High severity + Diversity in burn severity + Years since fire + Days since fledging + Ordinal fledging date + Region + Sex + Mass	313.9	7.9

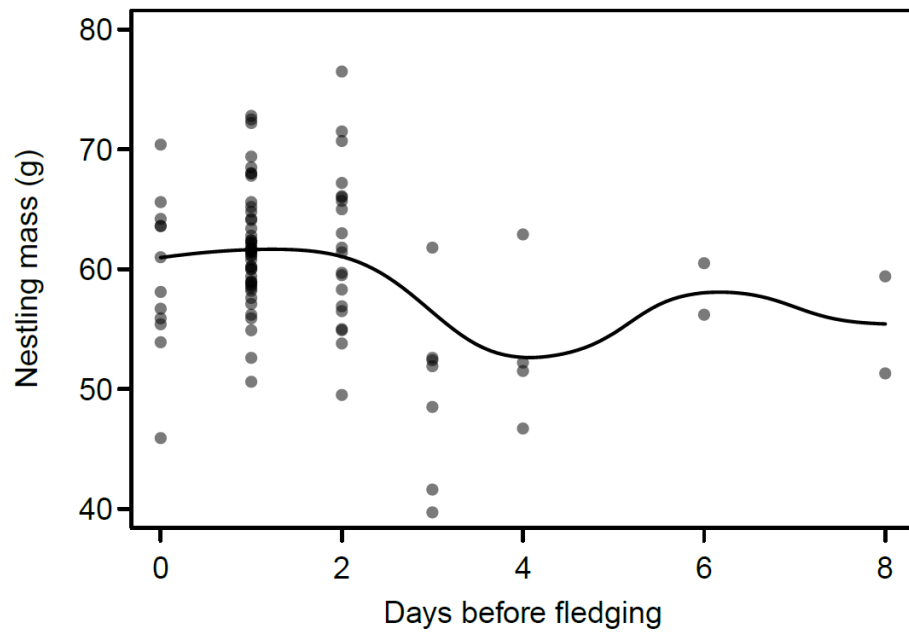


Figure S1. Mass of 84 nestling black-backed woodpeckers at the time of capture and tagging. Nestling mass was highly variable, with a slight increase in average mass 0-2 days before fledging. The black line shows a kernel smoothing function through observed means.

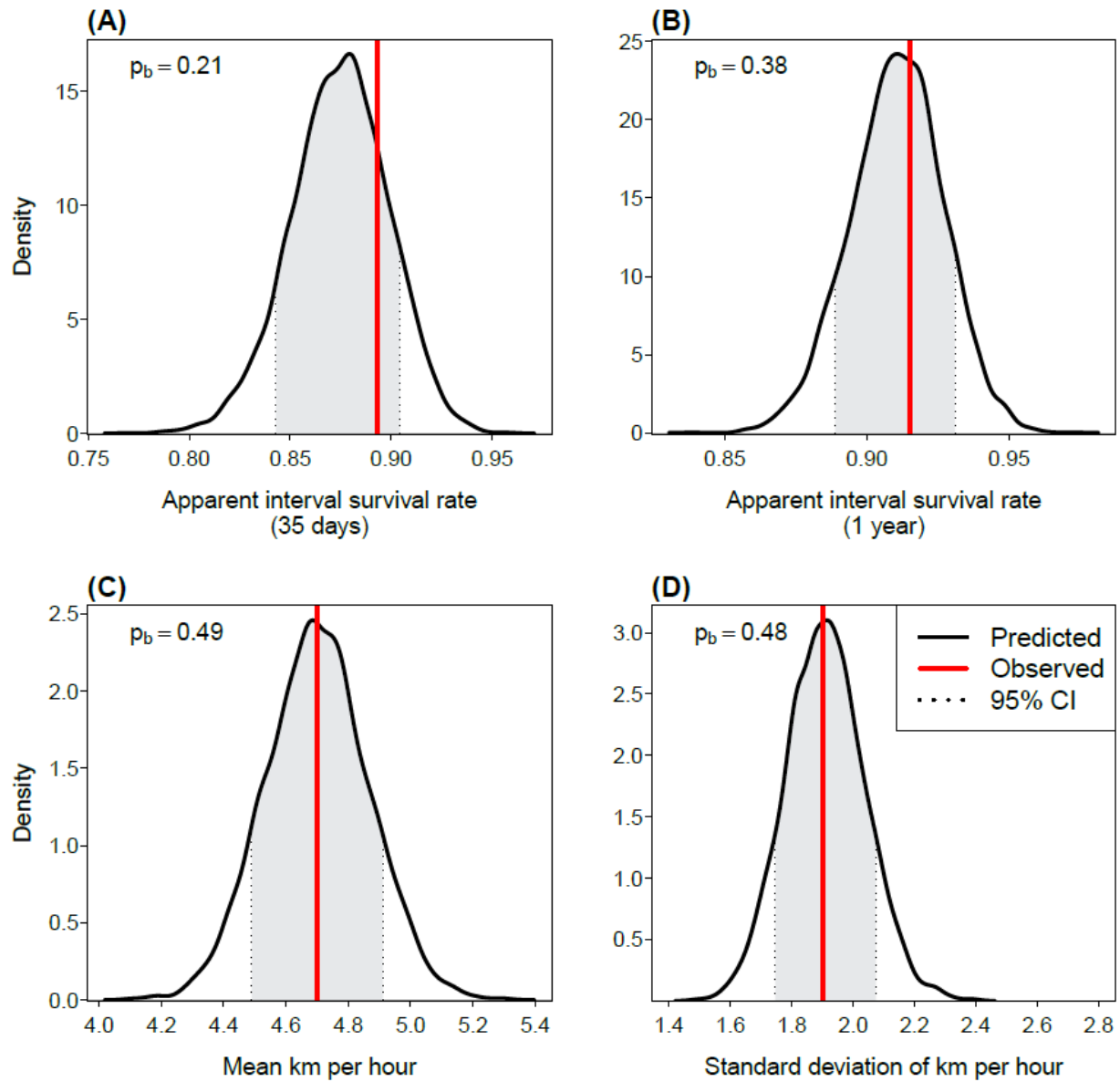


Figure S2. Posterior predictive checks indicated no evidence for lack of model fit for (A) the model of 35-day fledgling daily survival probability, (B) the model of juvenile annual survival probability, and (C, D) the model of fledgling movement rates. A test statistic was created for the two survival models based on the apparent mean interval survival rate. For the movement model, we used a test statistic calculated from the mean and standard deviation of log-transformed movement rates (km/hr). In each case, we simulated test statistics from the model posterior distribution (black line) along with 80% credible intervals (grey shading) and compared this distribution to the observed true test statistic (red line). Observed test statistics overlapping with 80% credible intervals fail to indicate a lack of fit ($p_b > 0.1$).

Chapter 4:

**Conditional natal dispersal provides mechanism for species tracking resource
pulses after fire**

LAY SUMMARY

When the best place to live is a moving target, animals need a strategy to follow. We show that black-backed woodpeckers possess dispersal strategies that enable them to follow unpredictable and temporary pulses of food and habitat created by fires in the western U.S. Juvenile woodpeckers were more likely to emigrate from older fires, where food is scarce, and juveniles selectively settled in burned forests. Woodpeckers from older fires also tended to disperse longer distances.

ABSTRACT

Animals that specialize on resource pulses face the challenge of tracking the rise and fall of resources across space and time. To combat these challenges, theory predicts that resource pulse specialists should use conditional dispersal strategies that allow them to emigrate from declining resource pulses and colonize new ones as they appear. We studied natal dispersal movements in the black-backed woodpecker (*Picoides arcticus*), a species known for its strong association with recent post-fire forests in western North America. We radio-tracked juveniles originating from seven burned areas and tested predictions that environmental and individual factors influence dispersal distance and emigration rates – investigating emigration while additionally accounting for imperfect detection with a novel Bayesian model. We found that juveniles were more likely to leave natal areas and disperse longer distances if they were heavier or hatched in older burned areas where resources are increasingly scarce. Juveniles were also more likely to leave their natal burn if they hatched in a nest closer to the fire perimeter. While dispersing across the landscape, black-backed woodpeckers selected for burned forest relative to unburned available habitat. Together, these results strongly support the hypothesis that this

species tracks resource pulses across fire-prone landscapes, with conditional natal dispersal acting as a mechanism for locating and colonizing newly burned areas. Lending empirical support to theoretical predictions, our findings highlight the potential role of conditional dispersal in the evolution of resource pulse specialization within a shifting mosaic of ephemeral habitat.

INTRODUCTION

Resource pulses are defined by the temporary availability of drastically elevated levels of food, habitat, or other population requirements that subsequently decline over time (Holt, 2008; Yang et al., 2008). While some species specialize in using resource pulses, the nature of these events – ephemeral, spatially limited, and often unpredictable – presents challenges that have long perplexed ecologists (Curran & Leighton, 2000; Thomas, 1994). Given these characteristics, resource pulses defy traditional models for how specialist species should efficiently move across landscapes and use resource patches (Jocque et al., 2010). Rather than rare or short-distance movement, resource pulse specialists are expected to exhibit movement-prone life history strategies for resource tracking consistent with three predictions. First, resource pulse specialists should show localized population trajectories that track the rise and fall of resource availability, as mediated by changes in immigration and emigration rates (Thomas, 1994; Yang et al., 2008). Second, these specialized consumers should be capable of directed dispersal over relatively long distances to track the shifting mosaic of resource pulses across the landscape (Johst et al., 2002; Reigada et al., 2015). Lastly, specialist species should exhibit conditional dispersal strategies that respond to external information such as environmental quality (condition-dependence), and individual factors, such as body size (phenotype-

dependence; Bowler and Benton 2005; Clobert et al. 2009). These predictions underscore the importance of dispersal behavior as a key parameter governing the distribution and metapopulation persistence of mobile species associated with transient, resource-rich habitats (Brotons et al., 2005; Johst et al., 2002; Reigada et al., 2015). While evidence supporting all three predictions has emerged for some invertebrates tracking resource pulses on small spatial scales (Hanski, 1999; Yang, 2006), direct tests using specialist vertebrate species across regional scales are rare.

Ecological disturbance is frequently overlooked as an agent of resource pulses, but many species benefit from elevated resource levels that develop during or following disturbance events. Disturbance regimes that alter landscape features may pave the way for a cascade of heightened resources in a successional context, as when immediate responses by one species produce a lagged positive response in other species through negative (e.g., predation) or positive (e.g., facilitation) interactions (He et al., 2019). Compared to conventional resource pulses, such as oak mast events – which combine low frequency, large magnitude, and short duration (Schmidt & Ostfeld, 2003; Yang et al., 2008) – resource pulses following disturbance may extend over one or more generations of consumers.

Ecological disturbances from wildfire can create local conditions with elevated resource availability for many years after fire, following the gradual attrition of dead trees or the shift to early successional vegetation (Grayson et al., 2019; Perry et al., 2011). Fire often creates discrete patches of elevated resource availability – such as canopy openings for aerial foragers and herbaceous plants (Perry et al., 2011; Smucker et al., 2005) – that host unique assemblages of plants and animals, with the frequency and magnitude of these resource pulses dependent on regional fire regimes (He et al., 2019). In western North America, the pulse of dead trees

following stand-replacing fire additionally attracts vast numbers of woodboring beetles which reproduce in dead and dying trees (Ray et al., 2019). Woodboring beetle larvae act as a pulsed food source for many woodpecker species, which in turn create nest cavities that are used by secondary cavity-nesting birds and mammals (Tarbill et al., 2015). Consequently, the ability of mobile species to find, colonize, and exploit post-fire resource pulses plays a key role in structuring the biotic community that arises after fire (Brotons et al., 2005; Nimmo et al., 2019).

Often called the most strongly fire-associated vertebrate in North America, the black-backed woodpecker (*Picoides arcticus*) colonizes burned forests rapidly after fire (Hutto, 2008; Tingley et al., 2018). Black-backed woodpeckers are strongly linked to post-fire areas, and they use standing dead trees (snags) for foraging on woodboring beetle larvae and excavating nest cavities (Rota et al., 2015; Stillman et al., 2019). However, the availability of woodboring beetle larvae and nesting substrates declines drastically in the decade after fire, following the gradual decay and attrition of snags. As expected by the first prediction for resource-pulse specialists, black-backed woodpecker populations within post-fire areas of western North America track these changes in resource availability, with local occupancy peaking between 3–5 years after fire and then gradually declining over the next 5–10 years (Taillie et al., 2018; Tingley et al., 2018). Given this population trajectory, theory predicts that black-backed woodpeckers also should exhibit dispersal strategies to track the rise and fall of fire-driven resource pulses. Black-backed woodpecker population age structure in burned forests – with higher proportions of younger individuals in more recent burns – suggests that natal dispersal may be an important demographic mechanism driving these population dynamics (Siegel et al., 2016). Additionally, because black-backed woodpeckers are relatively uncommon outside of burned forests in western North America (Tingley et al., 2020), burned forests are hypothesized to act as source

populations, with emigrants colonizing newly burned forests or persisting at low densities within the unburned matrix (Hutto, 2008; Nappi & Drapeau, 2009). Natal dispersal may be the key mechanism that allows this specialist to track the shifting mosaic of burned forests across the landscape and exploit post-fire resource pulses.

Natal dispersal involves the permanent movement from a natal to a breeding territory (Greenwood, 1980). Natal dispersal strategies evolve in response to a variety of ultimate factors, including inbreeding avoidance, conspecific competition, and correlations between intrinsic patch quality and fitness. In the context of patchy populations, natal dispersal frequently involves inter-patch movements consisting of three stages: (1) emigration, (2) transience, and (3) selection and immigration into a new patch (Bowler & Benton, 2005). Where resources decline predictably over time, organisms should exhibit plastic, conditional dispersal strategies that respond to variation in patch quality over the short term (Clobert et al., 2009; Thomas, 1994). Thus, animals tracking post-fire resource pulses should show variable emigration rates that respond to natal patch characteristics, such as time since fire, patch size, or habitat availability (Nimmo et al., 2019), in addition to social and physiological cues (Clobert et al., 2009; Kesler et al., 2010). Similar factors may govern the selection of new breeding territories, and we predict that dispersing post-fire specialists non-randomly immigrate into post-fire habitats relative to availability on the landscape.

Here, we use dispersal data from black-backed woodpeckers to empirically test the hypothesis that species specializing on temporary resource pulses exhibit condition- and phenotype-dependent dispersal strategies to track resources through space and time. While past work has postulated that this hypothesis may be true for black-backed woodpeckers (Pierson et al., 2013; Rota et al., 2014; Siegel et al., 2016; Tingley et al., 2018), direct studies of dispersal

behavior are lacking for this species, and some studies have argued that the species' occurrence patterns do not support the hypothesis for selection of post-fire forest during dispersal (Fogg et al., 2014). We predicted that black-backed woodpeckers engage in natal dispersal movements between burned areas and that dispersal behavior would respond to condition- and phenotype-dependent factors. To test this, we first assessed the effects of condition-dependent environmental factors (years since fire, fire size, distance to fire boundary, elevation) as well as phenotype-dependent individual factors (sex, body mass) on dispersal distances. Second, we developed a novel Bayesian model to evaluate how these factors influence the probability of dispersal away from the natal fire while accounting for the imperfect detection of dispersal events and making use of incomplete dispersal data. We additionally used simulations to test the prediction that dispersing individuals are more likely to settle in burned forest relative to its availability on the landscape.

METHODS

Study area and field methods

We used radio-telemetry to track black-backed woodpecker natal dispersal in montane regions of northern California (Sierra Nevada and Southern Cascade ranges) and central Washington, USA (Cascade range). All birds in this study originated from nests within burned areas of predominantly conifer forest spanning a gradient of 1–10 years since fire. In California, we tagged birds in three areas burned by wildfires that ranged from 162.6–311.1 km² in size: the Moonlight fire (burned in 2007), Chips fire (2012), and Bald fire (2014). In Washington, we tagged birds in three prescribed fires and one wildfire: Kaboom (2009), Angel 1 (2014), Angel 2 (2016), and Meeks (2015). The Washington fires were relatively small, ranging from 4.5–25.1

km², but still included patches of stand-replacing fire > 10 ha. Post-fire logging occurred in portions of California wildfires before and during the study, although our study sites focused on unlogged areas.

We captured nestlings just prior to expected fledging (mean = 1.6 days before fledging) during spring and summer 2016–2018. We used the hole-saw method to access nestlings (Ibarzabal & Tremblay, 2006), conducted standard measurements on each individual, and fit birds with 1.6-g connectivity tags (Model CTx Ag 392, Lotek Wireless Inc. Newmarket, Ontario, Canada) with an adjustable leg-loop harness made of elastic beading cord (Rappole & Tipton, 1991). CTx transmitters included a programmable on/off calendar schedule that extended battery life over a year post-deployment; we programmed each tag to transmit during three intervals: May–Aug, Sep.–Nov, and Apr–Jun. We coated transmitters in a thin layer of quick-dry epoxy as added protection against mechanical wear. Transmitters weighed less than 3% of average body mass to minimize impact on movement and survival (Fair et al., 2010). We marked nestlings with a unique combination of color bands and a numbered USGS leg band before returning them to their nest cavity.

We used a combination of on-the-ground radio tracking and aerial telemetry to track natal dispersal movements. We tracked fledglings from the ground every 3–5 days until early August to record location coordinates and visually confirm survival. We found that juveniles began to disperse in August and September, so we transitioned to a more intermittent tracking schedule based on the availability of aircraft, with the goal of locating each bird 3–5 times between August and November using two strategies: driving road networks with vehicle-mounted antennas, and fixed-wing aerial telemetry. Aerial telemetry flights included a series of concentric circles around previous locations and systematic search transects with 5-km spacing. We

concentrated flight effort within 35 km of natal sites, but specific searches sometimes extended out to >60 km from a bird's last known location. Programmable transmitters switched off during the winter to save battery life and turned back on the following spring, allowing us to use the same methods to locate birds approximately one year after fledging when most individuals engage in their first breeding attempt.

Over the course of this study, we conducted 15 fall aerial telemetry flights and 14 spring flights. Combined with on-the-ground search efforts, this yielded 5 possible re-sighting histories: (1) located in both fall and spring, (2) located in fall but missing in spring, (3) missing in fall but located in spring, (4) missing in both fall in spring, and (5) found dead during the study period. We recorded a death if remains were found with a transmitter or if the transmitter was found with evidence of predation (e.g., blood on harness, beak indentations on coating). We also recorded data from 4 color-banded individuals without transmitters that were opportunistically located one year after fledging, although these individuals were omitted from analysis where the inclusion of non-radio-tagged birds would introduce sampling bias.

In addition to searching for dispersing birds, we conducted a series of flights aimed at estimating the probability of transmitter detection from fixed-wing aircraft. The probability of detecting a transmitter on a single aerial survey was 0.82, and signals remained strong within 3 km of the transmitter. The probability of detection given two or three flights increased to 0.95 and 0.99, respectively. For more information on detection tests, see Appendix S1.

Field methods were approved by the University of Connecticut Animal Care and Use Committee (Protocol A16-008), the USFS Animal Care and Use Committee (2016-007), the California Department of Fish and Wildlife (Scientific Collecting Permit #SC-8645), the

Washington Department of Fish and Wildlife, and the USGS Bird Banding Laboratory (Permits 22423, 24061).

Distribution of dispersal distances

Although telemetry flights covered a vast search area, our observed dispersal distances showed a downward bias due to missing birds that likely flew beyond search boundaries. To build a distribution of dispersal distances, we applied a bias-correction method that uses interval-censored data to include information on birds with incomplete dispersal tracks (Paradis et al., 2002). This method provides added flexibility over area-ratio corrections, which require that binned dispersal distances have frequencies greater than 1 in the range of observed values (Baker et al., 1995; Cooper et al., 2008). The assumption of area-ratio corrections may be inappropriate for studies with small sample sizes or studies where dispersers may have traveled farther than the maximum observed distance, as in our case. Alternatively, interval-censored correction methods use data from individuals with known dispersal distances (uncensored data) as well as individuals with incomplete dispersal information (interval-censored data) to parameterize a bias-corrected distribution of dispersal distances. Interval-censored data comprise a minimum dispersal distance (observed or estimated) and a maximum dispersal distance, analogous to interval-censoring in survival studies (Paradis et al., 2002).

For each bird in our study with incomplete dispersal information, we estimated the minimum dispersal distance as the distance from the natal nest to the nearest area within potential habitat (i.e., >10% conifer canopy cover) that was not surveyed by aerial telemetry (Appendix S1: Figure S1). Although this method assumes complete detection within the search area, it provides a conservative approximation given that detection probability was high within the flight area and searches frequently extended well beyond the minimum distance (e.g.

estimated distance may correspond to a gap in the flight area) (Koenig et al., 1996). We used 100 km as a feasible maximum bound of dispersal distance based on observed records and genetic evidence from this species (Pierson et al., 2013; Rota, 2013; Yunick, 1985), and we tested the sensitivity of our inference to this cutoff (Appendix S2: Table S1). We fit four potential dispersal distributions – half-Cauchy, lognormal, normal, and Weibull – to the interval-censored data using the package “fitdistrplus” in the programming language R (Delignette-Muller & Dutang, 2015; R Core Team, 2020). For each distribution, we estimated parameters using a maximum likelihood approach and used the distribution with the lowest Akaike’s Information Criterion (AIC) for inference.

Modeling dispersal distance and dispersal probability

We tested for individual and environmental effects on three components of black-backed woodpecker dispersal behavior: (1) final dispersal distance, (2) fall dispersal status (individual either remained in the natal fire or dispersed out, see below), and (3) spring dispersal status. For birds with known post-dispersal locations ($n = 19$), we modeled dispersal distance as a function of covariates using a Bayesian linear regression model with a natural log-transformed response variable. Due to sample size constraints that limited power of multi-variate models, we built six candidate models, each with a single covariate based on *a priori* hypotheses (Appendix S2: Table S2). These covariates were nestling mass, nestling sex, distance from the nest to the perimeter of the fire area, elevation at the nest tree, years since fire, and size of the fire area. We did not include study region (California versus Washington) as a variable due to a strong correlation with fire size, which we considered to be a better justified hypothesis. All continuous variables were standardized by subtracting the mean and dividing by the standard deviation. Because nestlings were weighed at a range of days prior to fledging, we standardized raw mass

values by subtracting the mean mass of birds tagged 0–2 days before fledging and 3+ days before fledging separately. Mass of nestlings at capture was variable, with a slight increase in average mass 2 days before fledging (Stillman et al., 2021).

We developed a novel Bayesian model to examine the factors that influence fall and spring dispersal status while incorporating incomplete dispersal data and accounting for imperfect detection. This “false-positive event detection model” extends the occupancy modeling framework (MacKenzie et al., 2018) to cases where negative detections (0s) are known with certainty, and positive detections (1s) are either certain or uncertain. Here, the certainty of negative detections is distinct from traditional “false positive” models which typically include uncertainty in both 0s and 1s (Miller et al., 2011). We treated fall dispersal status as a binary response variable, where the observed value, y_i , for individual i is equal to 0 if a juvenile remained within the natal fire during the fall, and $y_i = 1$ if a juvenile dispersed away from the natal fire or if surveys failed to detect it within the fire boundary. To avoid counting potential prospecting movements, we recorded a dispersal event only if an individual remained outside the fire perimeter at the end of fall surveys. Similarly, we recorded spring dispersal status as $y_i = 0$ if a bird settled within the natal fire the following spring, and $y_i = 1$ if a bird settled outside of the natal fire boundary or remained undetected. Observations of emigration are assumed to be imperfectly observed representations of the true dispersal status for each individual, z_i . Thus, the observed dispersal status, y_i , is modeled as:

$$y_i \sim \text{Bernoulli}(z_i + (1 - z_i) * p_i)$$

where \mathbf{p} is a vector giving the measured probability of recording a false positive for each individual i . For example, an individual that remained undetected for two consecutive search flights would receive $p_i = 1 - 0.18^2 = 0.0324$, where 0.18 is the per-flight probability of

inferring that the species has left the study area (i.e., not detected) when in fact it has remained in the study area and went undetected. Likewise, an individual located with certainty outside of the natal fire or detected within the fire boundary would receive $p_i = 0$. In this way, our model incorporates observations from individuals with incomplete dispersal data, where either fall, spring, or both fall and spring locations are missing, while incorporating the probability of detecting missing birds during aerial telemetry flights. Thus, the true dispersal status for an individual, z_i , is modeled as, $z_i \sim \text{Bernoulli}(\varepsilon_i)$, where ε_i is the probability of dispersal away from the natal fire. We modeled the probability of dispersal separately for the spring and fall as a logit-linear function of one of the same six covariates (\mathbf{X}) described above, i.e. $\text{logit}(\varepsilon_i) = \beta_0 + \beta_1 X_i$. For all three model sets (dispersal distance, fall dispersal status, spring dispersal status), we compared models using leave-one-out cross validation (LOO) to estimate the pointwise out-of-sample prediction accuracy (Vehtari et al., 2018).

We fit models to the data using JAGS (Plummer, 2003) with the package ‘R2jags’ in R (Su & Yajima, 2015). In all cases we used vague priors: $\text{normal}(\mu = 0, \tau = 0.001)$ and $\text{gamma}(r = 0.001, \lambda = 0.001)$ for linear regression models, and $\text{normal}(\mu = 0, \tau = 0.2)$ for false-positive event detection models. We ran 3 chains of 15,000 iterations with a burn-in of 5000 and a thin rate of 20, yielding a final posterior sample of 1,500 across all chains. We visually inspected traceplots to assess chain convergence and confirmed that the Gelman-Rubin statistic was < 1.1 for every parameter estimate (Gelman et al. 2004). We used 95% Bayesian credible intervals on posterior samples to make inference on parameters. We evaluated model fit using Bayesian p-values for test statistics summarizing the posterior predictive distribution (Conn et al. 2018; see Appendix S2 for more information). JAGS code and input data for our models are available from the Dryad Digital Repository (available after publication).

Simulation analysis

To examine whether dispersing juveniles select for burned areas, we conducted a spatially explicit simulation analysis testing our empirical results versus a null model where dispersal is random with respect to the locations of burned habitat near the nest site. For each juvenile with a known post-dispersal location, we simulated 1,000 dispersal events originating from the natal nest with distances drawn from the parameterized dispersal distribution (see methods above) and recorded the number of individuals settling in each of ten 10-km concentric distance bands centered on the natal nest. For each distance band, we then calculated the proportion of potential breeding habitat burned by wildfire or prescribed fire within the last 10 years to estimate the number of simulated birds settling in burned forest under the null model. We compared the simulated number of juveniles settling in burned forest to the observed data and calculated the probability of observing our data under the null model. For further details see Appendix S1.

RESULTS

Out of 81 marked nestling black-backed woodpeckers in 7 different post-fire areas, our final dataset comprised 32 radio-tagged and 4 color-banded juveniles, each with confirmed survival to at least 35 days post-fledging. We successfully relocated 23 of these 36 individuals in the fall (including 4 confirmed deaths) and 22 birds the following spring (with 3 confirmed deaths). Juvenile black-backed woodpeckers frequently moved considerable distances, and over half of radio-tagged individuals with known spring locations dispersed greater than 10 km from their natal nest. Dispersal outcomes varied among individuals, including dispersal from the natal fire to a different fire (Figure 1a, d), dispersal from the natal fire to unburned forest (Figure 1b,

e), and dispersal from the natal territory to a different territory in the same fire (Figure 1c, f).

Dispersal events tended to occur in August and September when birds first became independent from parents.

Measured natal dispersal distances ranged from 1.6 km to 51.2 km, and the raw dispersal kernel showed high skewness and kurtosis statistics (2.4 and 10.4, respectively), indicating a fat-tailed distribution (Figure 2). The Weibull distribution provided the best fit to our interval-censored dispersal data (shape = 1.30 ± 0.24 , scale = 24.30 ± 4.62 ; Appendix S2: Table S1). Bias-corrected estimates yielded a median natal dispersal distance of 18.4 km, with 75% of individuals moving at least 9 km and 5% of dispersers moving greater than 50 km from natal territories (Figure 2).

Model comparisons indicated strong support ($\Delta\text{LOOIC} < 2$) for two variables influencing natal dispersal distance (Appendix S2: Table S3). First, natal dispersal distance showed a strong positive relationship with time since fire, with predicted mean dispersal distance increasing from 4 km to > 20 km as the number of years since the natal fire burned increased from 1 to 10 years. Second, natal dispersal distance increased as nestling mass increased (Figure 3).

The number of years since a fire burned also had a strong, positive effect on the probability that a juvenile left the natal fire in the fall (Figure 4a), and this was the only fall-dispersal model with $\Delta\text{LOOIC} < 2$ (Appendix S2: Table S4). A one-year increase in time since fire doubled the odds of leaving the natal fire (odds ratio = 2.14; 95% CrI = 1.21, 4.68).

Two candidate models of spring dispersal status had strong support: standardized nestling mass and distance to fire perimeter (Figure 4, Appendix S2: Table S5). Juveniles with higher mass prior to fledging were more likely to settle outside of natal fire boundaries, and each 1-g increase in mass increased the odds of settling outside the natal fire by a factor of 1.27 (95% CrI

= 1.04, 1.66). Juveniles with natal nest sites close to the fire perimeter were more likely to settle outside the natal fire (odds ratio = 0.93, 95% CrI = 0.84, 0.99). Posterior predictive checks demonstrated that models generally provided good fit to the data (Appendix S2: Figure S1, S2).

We found strong evidence that juvenile black-backed woodpeckers select for burned forests relative to available breeding habitat when dispersing across the landscape. Under the null model assumption that dispersal is random with respect to fire locations, our simulations predicted that a median of 11% of individuals (2 of 18) would have settled within burned forest (range 0–50%, Figure 5a), whether within the natal fire or in a different burned forest. By comparison, 78% of observed individuals (14 of 18) in our dataset settled in burned forest. There was no overlap between our null model simulations and our observed data, indicating that juvenile black-backed woodpeckers are much more likely to settle in burned forest relative to availability ($p < 0.001$). Among birds that left their natal fire and settled in a different post-fire forest ($n = 7$), our observations indicate a tendency to settle in fires that burned more recently than their natal fire (Figure 5b). Selected burns were a median of 5 years younger than natal burns, although limited sample sizes prevent robust estimates (one-sided sign test, $p = 0.11$).

DISCUSSION

Species that track post-fire resources face the challenge of locating and colonizing discrete, ephemeral habitat patches that appear unpredictably on the landscape. This differs substantially from many other species that track resources, such as migratory ungulates tracking the “green wave” of seasonally recurrent vegetation growth (Merkle et al., 2016). Our results provide empirical support for the hypothesis that conditional dispersal enables resource pulse specialists to track erratic resources through space and time. While past field and experimental

work has tested this hypothesis using a variety of invertebrate taxa (Hanski, 1999; Yang, 2006), our study presents novel evidence from a vertebrate associated with post-fire resource pulses. Natal dispersal distances in black-backed woodpeckers were longer for heavier individuals and for individuals from older post-fire areas. Relatedly, juveniles were more likely to leave their natal fire if the fire was older, their body mass was greater, or they came from a nest closer to the fire perimeter. Our finding that dispersing juveniles selectively immigrate into burned forests over all other types of available habitat lends further support to the hypothesis that natal dispersal strategies in black-backed woodpeckers have evolved in response to the shifting mosaic of resource pulses in fire-prone landscapes.

The challenge of imperfect detection in studying dispersal

Despite the demonstrated importance of dispersal to gene flow, metapopulation dynamics, and species distributions (Bowler & Benton, 2005; Johst et al., 2002), the drivers of dispersal behavior remain enigmatic in many species. This is partially because quantities like dispersal rates and dispersal distances are exceedingly difficult to measure accurately in the field, particularly for lightweight and highly mobile species like birds (Koenig et al., 1996). Incomplete datasets and partial dispersal tracks are the norm, and there has been considerable effort to develop analytical approaches to glean biological information from imperfectly detected datasets. Bias-correction methods can be applied to scale observed dispersal distances according to some probability of detection (Baker et al., 1995; Cooper et al., 2008), although these methods fail to make use of the partial information researchers might have on certain individuals (e.g., last recorded location). Interval-censored data can be used to fit distributions to datasets with partial dispersal tracks (Paradis et al., 2002), but researchers are often precluded from using these incomplete datasets when assessing the factors that may drive condition- or phenotype-

dependent dispersal and emigration rates. Integrating data on observed emigration rates with estimated probabilities of detection presents a novel opportunity to analyze the proximate factors governing dispersal probabilities.

In this study, we developed a false-positive event detection model to evaluate the conditions that influence emigration rates while accounting for imperfect detection during aerial surveys. Even with fixed-wing aerial telemetry over large study areas, detection probability may still downwardly bias dispersal observations, and we encourage future studies to incorporate tests to estimate detection probability into their study designs. The false-positive event detection model employed here could be easily extended to other datasets involving imperfectly detected animal emigration events, such as the movement behavior of birds at migration stopover locations. While the miniaturization of robust global positioning system loggers and transmitters may eventually solve the quandary of lost long-distance dispersers, for many species – including the vast majority of birds – our ability to track where individuals have dispersed remains limited by where we can physically search for signals.

Long-distance movement and environmental effects on dispersal

Black-backed woodpecker dispersal distances measured in this study (median = 18.4 km) exceed typical distances reported from other North American woodpecker species and showed evidence for a “fat-tailed” dispersal kernel after correcting for detection bias. In comparison, a long-term study of red-cockaded woodpeckers (*Leuconotopicus borealis*) – a cooperatively-breeding fire-associated species – documented median natal dispersal distances from 2.9–3.3 km (Kesler et al., 2010). Natal dispersal distances for cooperatively-breeding acorn woodpeckers (*Melanerpes formicivorus*) averaged less than 1 km (Koenig et al., 2000). Although not directly tied to natal movements, some seed-eating birds in boreal biomes are known to respond to

spatiotemporal fluctuations in annual food availability across larger scales (100s of km) via facultative migration (Koenig & Knops, 2001; Newton, 2012). While our study focused on natal dispersal movements in response to localized resource pulses, black-backed woodpeckers – particularly in eastern North America – may also engage in long-distance irruptive movements beyond normal range limits (Rota et al., 2015; Yunick, 1985).

Theoretical work has demonstrated that dispersal in dynamic landscapes can increase metapopulation persistence through increased couplings between disparate patches (Johst et al., 2002), suggesting that inter-patch distances between burned forests may be a selective force driving the evolution of high dispersal capacity in black-backed woodpeckers, and potentially other post-fire specialists. In addition, matrix permeability between patches can have strong effects on dispersal distance (Ricketts, 2001). Forested regions of the western USA have recently experienced increased tree mortality due to drought and bark beetle outbreaks (Preisler et al., 2017), which may increase matrix permeability for dispersing black-backed woodpeckers. The potential role of matrix habitat on dispersal behavior also highlights the importance of forest management actions that modify burned and unburned forests, as these actions could have potential downstream effects on metapopulation dynamics and the spatial genetic structure of species tracking post-fire resources (Pierson et al., 2013).

Our results show evidence for condition-dependent dispersal strategies in response to successional changes in habitat quality as post-fire resources decline in the years following fire. Increasing emigration rates in older post-fire forests likely reflect the process of resource pulse attenuation as snags decay and food availability declines (Grayson et al., 2019; Ray et al., 2019). Although more years since fire increased the probability of juveniles emigrating in the fall, this measure did not have a strong effect on whether or not a juvenile settled within the natal fire the

following spring. This counter-intuitive result may stem from the availability of recently burned forests on the landscape – if juveniles do not find suitable breeding areas during fall dispersal, they may return to their natal fire. We observed this particular behavior several times in our dataset, including one individual that dispersed from a 10-year old fire into an unburned matrix with low availability of new fires, only to return to its natal fire by the following spring (Figure 1c).

In addition to individuals seeking out non-natal burned forest, juveniles that dispersed from one post-fire patch to another predominantly selected areas that had burned more recently than their natal patch (Figure 5b). This apparent selection for “greener pastures” – which deserves to be secondarily evaluated with larger sample sizes – raises questions about how individuals may integrate information about habitat quality while moving across the landscape. If black-backed woodpeckers selectively search for higher-quality burned patches as they disperse, then an even greater mystery is how they might find such patches. Given that natal dispersal generally occurs during the active fire season in our study regions (Tingley et al. 2018), it is possible that juveniles could use olfactory or other cues to find very recently burned forests or even forest fires in progress. Indeed, anecdotal observations in the course of this study suggest that juveniles may actively orient towards new fires – we observed two tagged individuals that emigrated from an old fire to a new prescribed fire 10 km away, arriving within 3 weeks of the burn.

Relationship between body mass and dispersal

Body mass is sometimes expected to have a negative relationship with dispersal in resource-limited systems because smaller, competitively-inferior individuals are excluded from high-quality habitats close to the natal site (Bowler & Benton, 2005; Waters et al., 2013). We

found the opposite pattern in black-backed woodpeckers, where individuals with higher nestling body mass dispersed farther and were more likely to settle outside of the natal fire. The reversal of this established pattern may be due to the location of “high-quality” habitat relative to natal territories. The fitness benefits of seeking a new resource pulse may outweigh the benefits of remaining in a familiar patch with increasingly scarce resources, particularly for juveniles in older fires. If, in a constantly attenuating, resource-pulse situation, the “high-quality” habitat frequently exists outside the natal patch, then the phenomenon observed here could arise. Larger individuals, which have more reserves for energetically costly dispersal, may gain a competitive advantage if they are capable of immigrating into a more recent burn.

Moreover, the potential interaction between time, habitat quality, and parental experience yields an intriguing hypothesis. In contrast to movement-prone juveniles, adult black-backed woodpeckers are generally site-faithful (Rota, 2013), and older post-fire forests tend to have older adults, which can live up to at least 8 years (Siegel et al., 2016). Given that adult breeding experience generally correlates with growth and survival of young (Perrins, 1970), we predict that nestlings in older fires may have higher body mass than nestlings from young parents in newer fires, despite the general decline in available high-quality habitat within these older fires. If true, this causal chain suggests that older fires may produce larger juveniles that are physiologically predisposed to disperse from the natal patch in response to other proximate factors like territory competition or resource availability. Indeed, we found a weak, positive correlation ($r = 0.30$, $p = 0.07$) between time since fire and nestling mass in our dataset, lending preliminary evidence to support this hypothesis. A similar hypothesis is that young black-backed woodpeckers from older fires may be predisposed to disperse via maternal effects. This phenomenon has been documented in the dispersal polymorphism of western bluebirds (*Sialia*

mexicana), where breeding females adjust egg-laying order in a way that leads to dispersal-prone, aggressive male offspring when resources are scarce (Duckworth, 2009). While this hypothesis warrants further investigation, we note that our study did not detect any relationships between juvenile sex and dispersal behavior.

Population dynamics and resource pulses

Local population trajectories in black-backed woodpeckers track the pulse and decline of post-fire resources, but the mechanisms underlying these dynamics have remained elusive (Tingley et al., 2018). Previous research has shown limited effects of years since fire on nest survival, juvenile survival, adult survival, and adult breeding dispersal (Rota et al., 2015; Rota, 2013; Stillman et al., 2019, 2021). Our results suggest that natal dispersal may be the primary demographic mechanism driving the local population dynamics of this resource pulse specialist. We hypothesize that rapid post-fire colonization can be largely attributed to relatively long-distance, directed movements by juveniles dispersing from older burns nearby, although some colonizers may also originate from nearby unburned forest. Initial increases in woodpecker density in early post-fire years may stem from juvenile recruitment and continued colonization, while decreases in density > 5 years post-fire may reflect increased juvenile emigration rates as resources wane. Similar dynamics are likely at play in other resource pulse specialists, where natal dispersal behavior may allow specialists to locate and colonize new resource pulses while also tracking local declines in resources through conditional emigration (Holt, 2008; Yang et al., 2008). Consistent with predictions from theory (Johst et al., 2002; Reigada et al., 2015), our empirical results suggest that natal dispersal may be a key parameter for the evolution of resource specialization in a shifting habitat mosaic.

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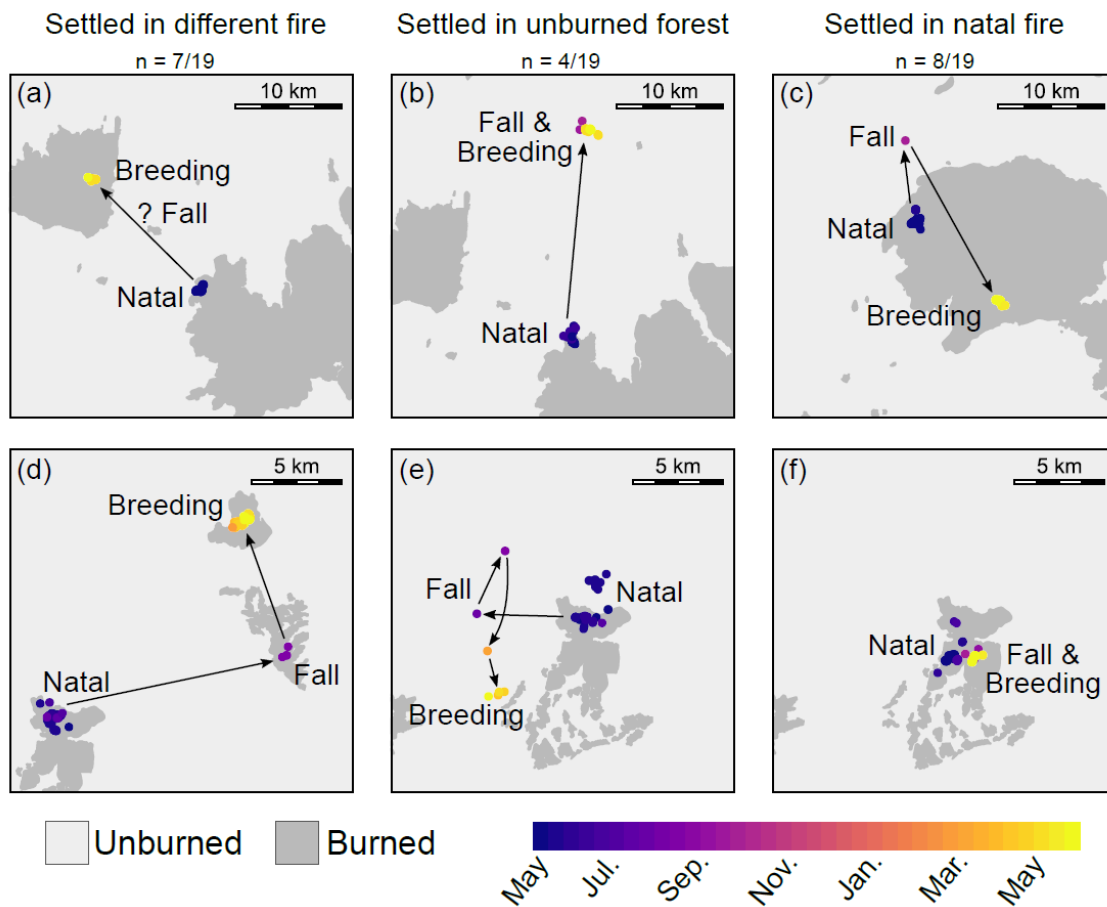


Figure 1. Example natal dispersal tracks for six black-backed woodpeckers in California (top row) and Washington, USA (bottom row). All juveniles originated from natal territories in burned forest, but dispersal strategies showed wide variation: (a, d) juvenile disperses from natal fire to a different burned forest, (b, e) juvenile disperses from natal fire and settles in unburned forest, and (c, f) juvenile disperses to a breeding territory within its natal burned area.

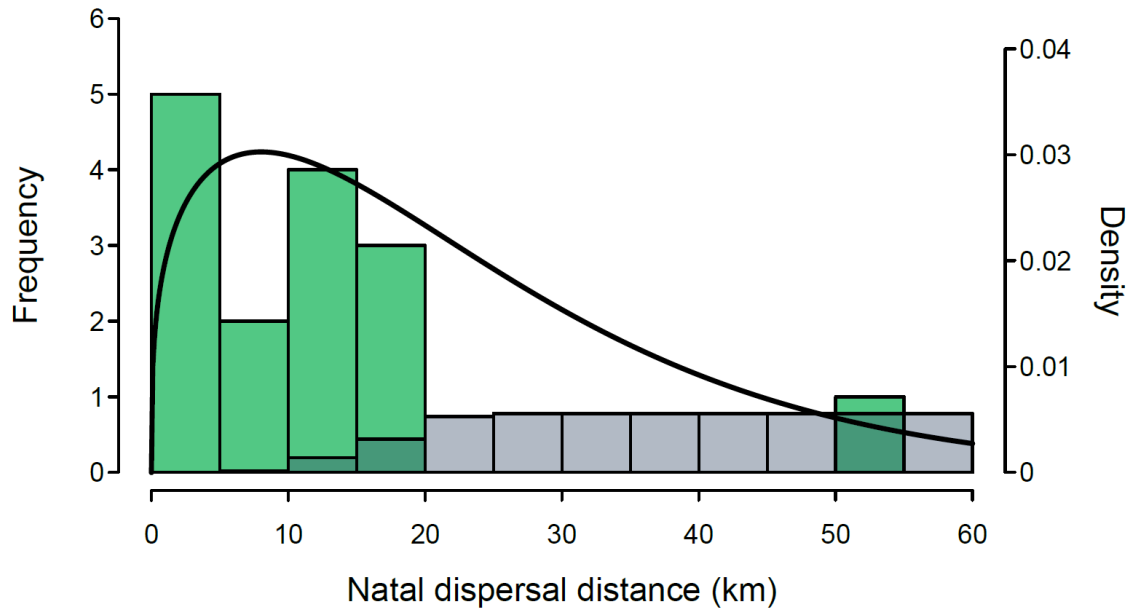


Figure 2. Distribution of black-backed woodpecker natal dispersal distances. Green bars show raw data (left axis) from 15 individuals with known dispersal distances, while overlaid gray bars indicate the aggregate probability density for 13 interval-censored individuals (right axis). The line shows the best-fit Weibull distribution corrected for sampling bias using both observed dispersal distances and interval-censored data from missing birds.

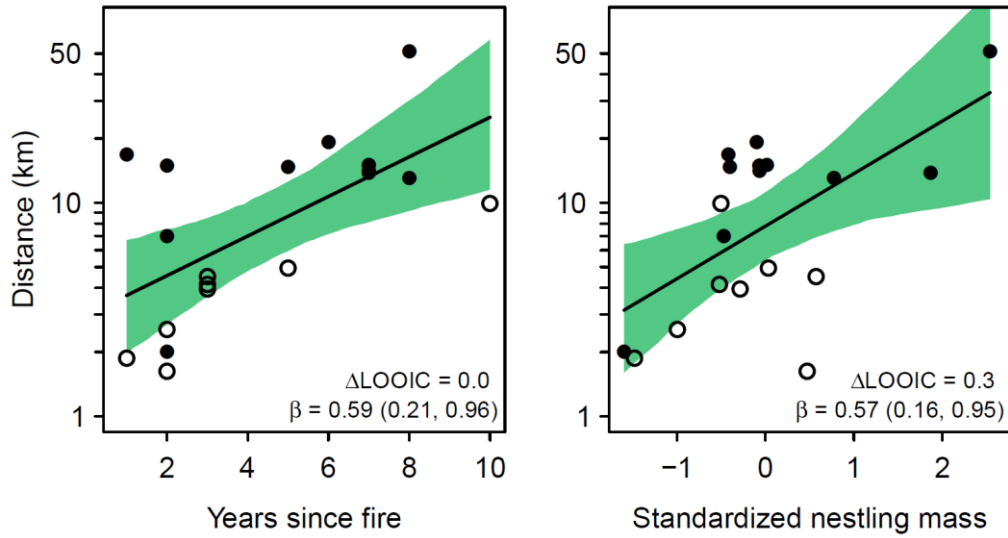


Figure 3. Model selection results indicated strong support for two variables influencing natal dispersal distance: the number of years since the natal fire burned, and the standardized mass of the dispersing individual. Filled dots show birds that settled outside of the natal fire, and open dots are birds that settled within the natal fire. ΔLOOIC values give the difference between each model and the model with the lowest LOOIC. Slope estimates are shown with 95% credible intervals.

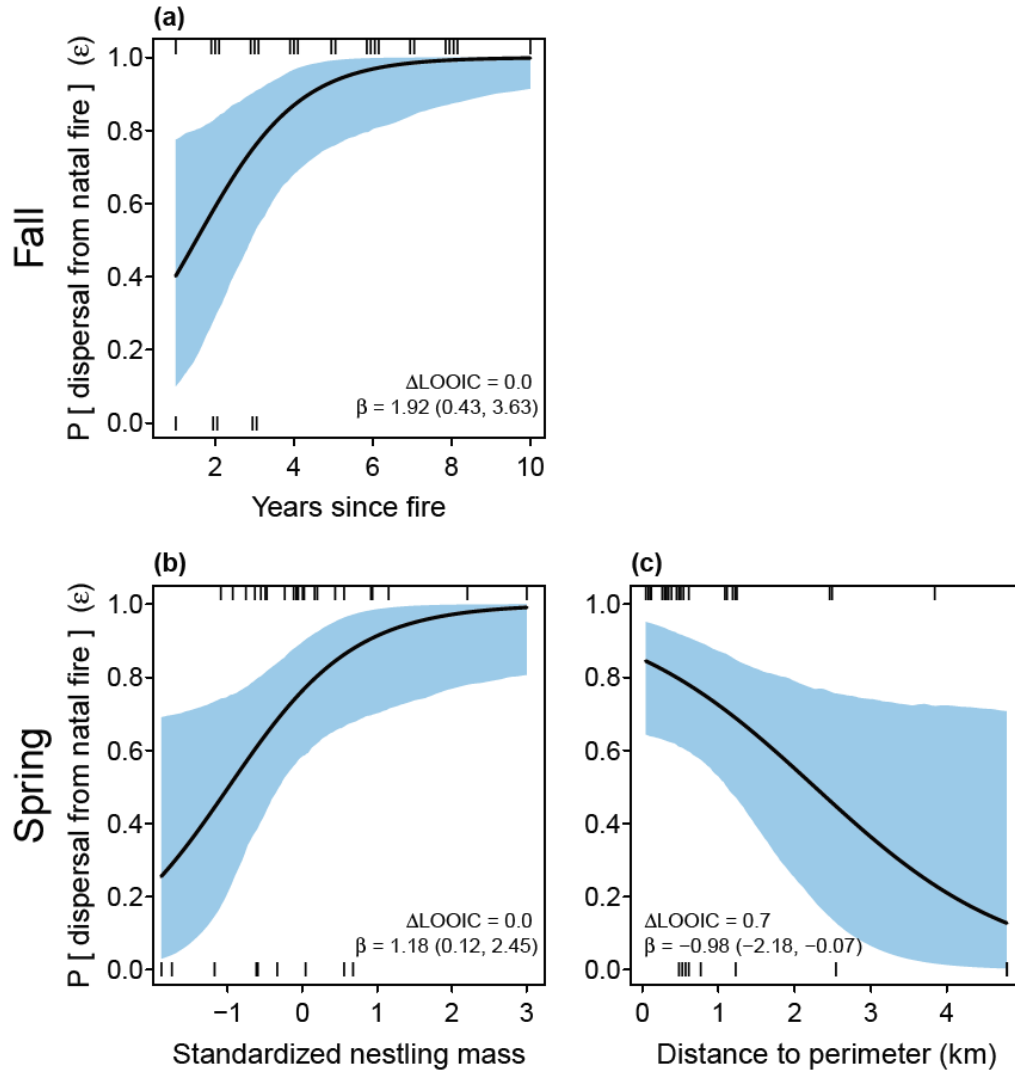


Figure 4. Modeled relationships showing the results of top model(s) for (a) the probability of a juvenile black-backed woodpecker dispersing away from its natal burned area in the fall, and (b, c) the probability of settling outside the natal fire in spring, accounting for false positives. Data rugs show naïve occurrence, where 0 = within natal fire, and 1 = outside of natal fire (jittered to enhance visibility). ΔLOOIC values give the difference between each model and the model with the lowest LOOIC, and slope estimates are shown with 95% credible intervals.

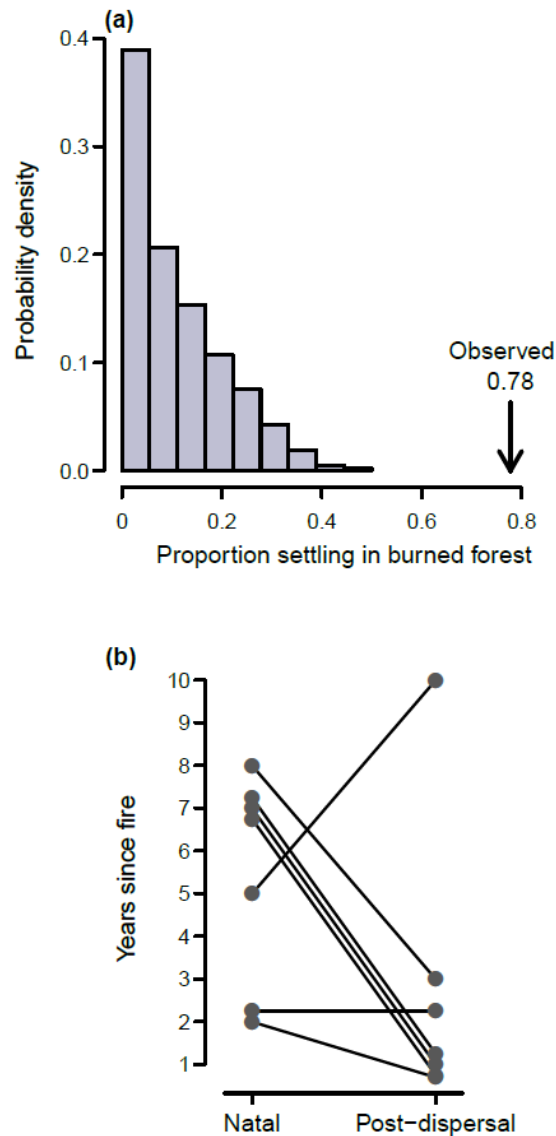


Figure 5. Simulated and observed data showing black-backed woodpecker selection for newly burned forests during natal dispersal. The histogram in (a) shows the number of expected individuals settling in burned forest from a simulation analysis under a null model assumption with no directional selection for burned forest. These values are compared to the observed data, where 14 of 18 birds settled in burned forest. Panel (b) compares years since fire between natal and post-dispersal habitat for birds that dispersed out of the natal fire and settled in a different burned area ($n = 7$). Years since fire values are jittered on the y-axis to enhance visibility.

Appendix S1

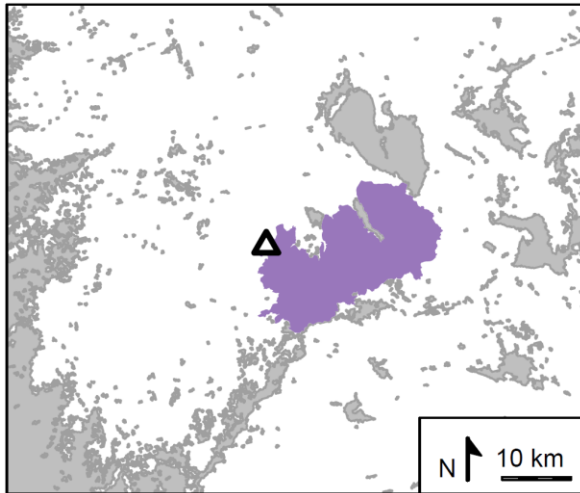
SUPPLEMENTAL METHODS

Transmitter detection tests for aerial telemetry

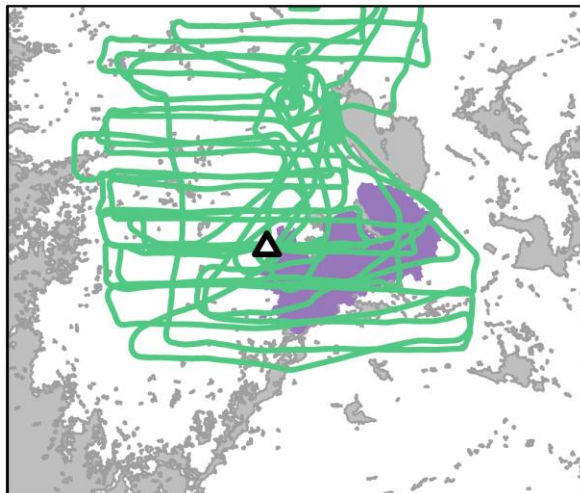
In addition to the 29 aerial telemetry flights that we conducted while searching for tagged birds, we conducted two aerial telemetry flights aimed at estimating the probability of transmitter detection from fixed-wing aircraft. For each detection test, we placed 5–6 transmitters within the search area by randomly assigning coordinates within a 100-m buffer of a spatial road layer. We placed one transmitter at each location and varied the position of transmitters to mimic real situations in the field. Some transmitters were attached vertically to a tree trunk to mimic live birds, while others were placed on the ground to mimic depredated birds.

Aerial telemetry tests were completed by an observer who did not know the true locations of transmitters or the number of active transmitters in the search area. We gave the observer a list of 10–11 possible frequencies to search for, although only 5–6 represented active transmitters. These conditions reflected the average number of birds an observer would search for during a normal survey. After flying a normal survey route, we found that observers were successful in locating 9 out of 11 active transmitters. This yields a transmitter detection probability of 0.82 for a single flight under average field conditions.

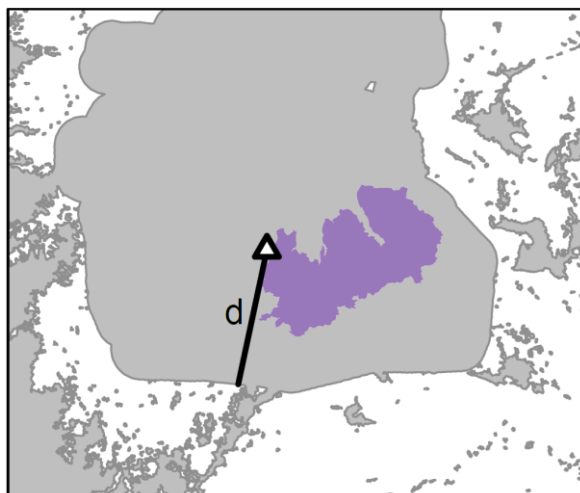
Minimum estimated dispersal distance



(1) An example natal fire (Chips fire) is shown in purple and the triangle (Δ) gives the natal nest location for an example juvenile. Gray shading represents areas of unsuitable breeding habitat, defined as areas with < 10% canopy cover of coniferous forest (chaparral, sagebrush steppe, pasture, marshes, and lakes).



(2) Green lines show the paths of three aerial telemetry flights that searched for the juvenile, without success. We plotted a 3-km buffer around flight paths and merged flight polygons to create an individual-specific search area boundary.



(3) Gray shading represents the union between areas of unsuitable breeding habitat and the search area polygon from above. There is a high probability that the juvenile has dispersed a minimum distance, d , spanning from the nest to the nearest edge of the gray shading. We used this value to define the left side, or lower limit, of interval-censored observations.

Figure S1. For birds in our study with incomplete dispersal information, we estimated a minimum dispersal distance using spatially explicit data on habitat suitability and the extent of our search area. We outline the method using an example from our dataset. First, we created a spatial layer containing “unsuitable” breeding habitat for black-backed woodpeckers, defined as areas with <10% canopy cover of coniferous trees based on gradient nearest neighbor forest structure maps (available at <https://lemma.forestry.oregonstate.edu/data>). We used a 10% cutoff because it adequately excluded habitat types where breeding black-backed woodpeckers are absent (e.g. pasture), while liberally including a wide range of forest types. Next, we plotted a 3-km buffer around flight paths and merged flight polygons to create an individual-specific search area boundary. Last, we recorded the minimum dispersal distance, d , for each woodpecker as the distance from the natal nest to the nearest area within potential habitat that was not surveyed during a search flight.

Simulation analysis

We used a spatially explicit simulation to test whether dispersing juvenile black-backed woodpeckers select for burned areas relative to their availability on the landscape. Our approach can be conceptualized as simulating 1,000 dispersal events for each juvenile with a known post-dispersal location under the assumption that post-dispersal settlement is independent from the locations of areas burned by wildfire and prescribed fire.

For each juvenile, we probabilistically drew 1,000 dispersal distances from the Weibull distribution parameterized using interval-censored data from this study. Next, we binned the dispersal distances into 10 10-km distance bands using concentric circles centered on the natal nest. Within each distance band, we used the proportion of potential breeding habitat burned by wildfire or prescribed fire within the last 10 years to estimate the number of birds within that distance band expected to settle in burned forest by random chance. We excluded unsuitable breeding habitat by omitting areas with < 10% coniferous canopy cover, and proportions represent the amount of burned potential habitat relative to available potential habitat within each distance band. Burn perimeter data were collected from the Fire and Resource Assessment Program (FRAP: <https://frap.fire.ca.gov/>), the Monitoring Trends in Burn Severity database (MTBS: <https://www.mtbs.gov/>), and the USDA Forest Service FACTS database for California (<https://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=STELPRDB5327833>) and Washington (<https://data.fs.usda.gov/geodata/edw/datasets.php>). We omitted one individual from the analysis due to a lack of updated spatial data, giving a sample size of 18 observed post-dispersal locations and 18,000 simulated post-dispersal locations.

Appendix S2

Table S1. We parameterized the natal dispersal kernel for black-backed woodpeckers using a combination of fully observed and interval-censored data. For the 13 individuals with incomplete dispersal data, we calculated an interval bounded on the left by the minimum estimated dispersal distance and on the right by a maximum cutoff (100 km) based on previous literature (Yunick 1985, Rota 2013, Pierson et al. 2013). To test the effect of this upper threshold on our inference, we replicated this analysis with two alternative thresholds: 80 km and 60 km. In all cases the Weibull distribution provided the best fit to the data.

Distribution	100 km cutoff	80 km cutoff	60 km cutoff
Weibull	Shape: 1.30 Scale: 24.30 AIC: 131.8	Shape: 1.35 Scale: 23.67 AIC: 132.0	Shape: 1.43 Scale: 22.53 AIC: 133.0
Lognormal	Meanlog: 2.77 SDlog: 1.00 AIC: 135.3	Meanlog: 2.74 SDlog: 0.98 AIC: 136.4	Meanlog: 2.70 SDlog: 0.94 AIC: 138.6
Half-Cauchy	Sigma: 17.94 AIC: 138.2	Sigma: 17.52 AIC: 140.0	Sigma: 16.87 AIC: 143.18
Normal	Mean: 20.07 SD: 13.17 AIC: 139.1	Mean: 20.06 SD: 13.16 AIC: 139.1	Mean: 19.97 SD: 13.04 AIC: 139.1

Table S2. *A priori* hypotheses for the six covariates used in models of (1) final dispersal distance, (2) fall dispersal status, and (3) spring dispersal status. Models of fall and spring dispersal status estimate the probability of emigrating from the natal burned area. Here, we refer to all three response variables collectively as “dispersal”.

Variable	Hypothesized relationship
<i>Standardized nestling mass</i>	Dispersal will decrease with increasing nestling mass because larger juveniles are able to compete for high-quality habitats close to the natal site. Alternatively, there may be a positive relationship between dispersal and mass if higher quality habitat exists outside of the natal patch and larger individuals have the energetic capacity to disperse and colonize it.
<i>Sex</i>	Dispersal is higher for males compared to females, consistent with the genetic evidence for male-biased dispersal in this species (Pierson et al. 2013).
<i>Distance from perimeter</i>	Dispersal is higher for juveniles from nests located closer to the fire perimeter because these individuals will travel less distance through potential high-quality habitat (i.e., burned forest) before emigrating from the natal fire and because natal home ranges may overlap unburned forest with low resource density.
<i>Elevation</i>	Previous research has shown a positive relationship between elevation and black-backed woodpecker occupancy (Tingley et al. 2018), suggesting that higher elevation sites provide greater access to suitable breeding habitat. Thus, we predict that dispersal is lower for juveniles at higher elevations because there is more available suitable habitat.
<i>Years since fire</i>	Dispersal will increase with increasing time since fire because snags and food resources gradually deteriorate over time in post-fire areas.
<i>Fire size</i>	Dispersal will increase in smaller post-fire areas because smaller fires are more quickly saturated with black-backed woodpecker territories, forcing more juveniles to settle outside of the natal fire.

Table S3. Model selection results and coefficient estimates for six candidate models of black-backed woodpecker natal dispersal distance.

Covariate	Estimate (95% CrI)	LOOIC	ΔLOOIC
<i>Distance ~ Years since fire</i>		48.2	0
Intercept	8.94 (8.57, 9.31)		
Time since fire	0.59 (0.21, 0.96)		
<i>Distance ~ Standardized nestling mass</i>		48.5	0.3
Intercept	8.96 (8.59, 9.33)		
Standardized nestling mass	0.57 (0.16, 0.95)		
<i>Distance ~ Distance from perimeter</i>		55.3	7.1
Intercept	8.95 (8.46, 9.39)		
Distance from perimeter	-0.23 (-0.67, 0.26)		
<i>Distance ~ Elevation</i>		56.2	8.0
Intercept	8.95 (8.51, 9.43)		
Elevation	0.12 (-0.36, 0.62)		
<i>Distance ~ Sex</i>		56.7	8.5
Intercept	8.47 (7.08, 9.83)		
Sex	0.34 (-0.63, 1.33)		
<i>Distance ~ Fire size</i>		56.7	8.5
Intercept	8.93 (8.44, 9.40)		
Fire size	0.11 (-0.38, 0.58)		

Notes: We made inference using candidate models that were within two Δ LOOIC of the top model. Coefficient estimates with 95% CrIs that do not overlap 0 are shown in bold. We considered candidate models within 2 Δ LOOIC values of the “top” model to have strong support, and we used all models with Δ LOOIC < 2 for inference.

Table S4. Model selection results and coefficient estimates for six candidate models describing the probability of juvenile black-backed woodpeckers dispersing and remaining outside of their natal fire in the fall.

Covariate	Estimate (95% CrI)	LOOIC	ΔLOOIC
<i>Dispersal ~ Years since fire</i>		21.3	0
Intercept	2.36 (1.02, 3.93)		
Time since fire	1.92 (0.43, 3.63)		
<i>Dispersal ~ Standardized nestling mass</i>		25.9	4.6
Intercept	1.86 (0.78, 3.16)		
Standardized nestling mass	1.38 (-0.03, 3.01)		
<i>Dispersal ~ Distance from perimeter</i>		28.6	7.3
Intercept	1.59 (0.60, 2.79)		
Distance from per.	-0.77 (-1.92, 0.22)		
<i>Dispersal ~ Fire size</i>		28.6	7.3
Intercept	1.69 (0.65, 2.88)		
Fire size	0.69 (-0.43, 2.03)		
<i>Dispersal ~ Elevation</i>		29.2	7.9
Intercept	1.61 (0.66, 2.73)		
Elevation	0.47 (-0.54, 1.60)		
<i>Dispersal ~ Sex</i>		29.5	8.2
Intercept	0.64 (-1.56, 2.83)		
Sex	0.65 (-0.89, 2.33)		

Notes: We made inference using the top model only. Coefficient estimates with 95% CrIs that do not overlap 0 are shown in bold. We considered candidate models within 2 ΔLOOIC values of the “top” model to have strong support, and we used all models with ΔLOOIC < 2 for inference

Table S5. Model selection results and coefficient estimates for six candidate models describing the probability of juvenile black-backed woodpeckers settling outside of their natal fire in the spring.

Covariate	Estimate (95% CrI)	LOOIC	ΔLOOIC
<i>Dispersal ~ Standardized nestling mass</i>		36.9	0
Intercept	1.17 (0.34, 2.15)		
Standardized nestling mass	1.18 (0.12, 2.45)		
<i>Dispersal ~ Distance from perimeter</i>		37.6	0.7
Intercept	0.87 (-0.01, 1.83)		
Distance from per.	-0.98 (-2.18, -0.07)		
<i>Dispersal ~ Years since fire</i>		39.8	2.9
Intercept	1.04 (0.21, 1.91)		
Time since fire	0.74 (-0.10, 1.70)		
<i>Dispersal ~ Sex</i>		39.8	2.9
Intercept	-0.28 (-2.34, 1.79)		
Sex	0.85 (-0.55, 2.29)		
<i>Dispersal ~ Elevation</i>		41.6	4.7
Intercept	0.92 (0.20, 1.77)		
Elevation	0.07 (-0.72, 0.85)		
<i>Dispersal ~ Fire size</i>		42.8	4.9
Intercept	0.92 (0.15, 1.77)		
Fire size	-0.03 (-0.72, 0.85)		

Notes: We made inference using candidate models that were within two ΔLOOIC of the top model. Coefficient estimates with 95% CrIs that do not overlap 0 are shown in bold. We considered candidate models within 2 ΔLOOIC values of the “top” model to have strong support, and we used all models with ΔLOOIC < 2 for inference

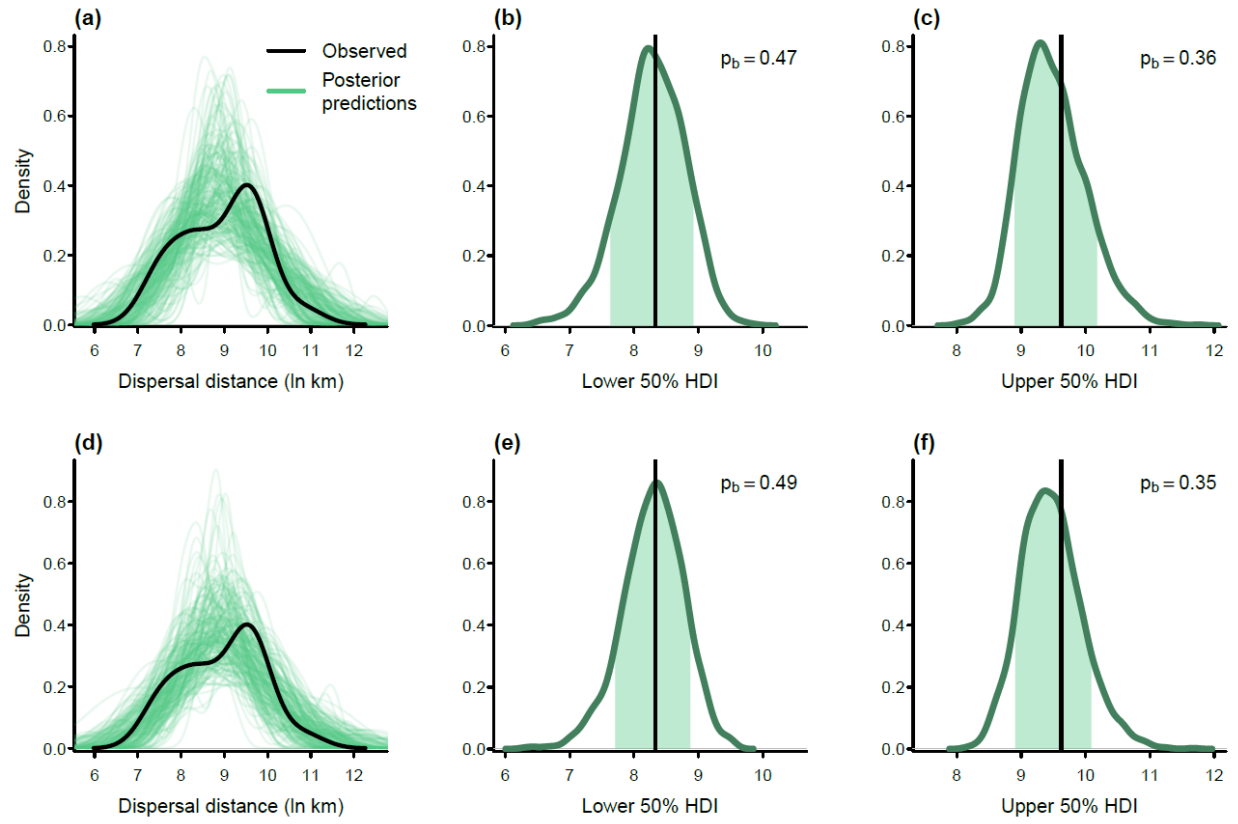


Figure S1. Posterior predictive checks for two models of natal dispersal distance. Panels a–c show checks for a model containing years since fire, and panels d–f show checks for a model containing standardized nestling mass. For each model, we first plotted the posterior density of predictions against observed data to highlight areas of potential lack-of-fit (a, d). Next, we conducted checks using two test statistics representing the lower and upper bounds of the 50% highest density interval (HDI) for observed and predicted data (b, c, e, f). In each case, we simulated test statistics from the model posterior distribution (green line) along with 80% credible intervals (green shading) and compared this distribution to the observed true test statistic (black line). Observed test statistics overlapping with 80% credible intervals fail to indicate a lack of fit ($p_b > 0.1$), although tests based on the upper 50% HDI indicated a slight tendency for the model to underpredict data in the right tail of the dispersal distribution (years since fire $p_b = 0.36$, nestling mass $p_b = 0.35$).

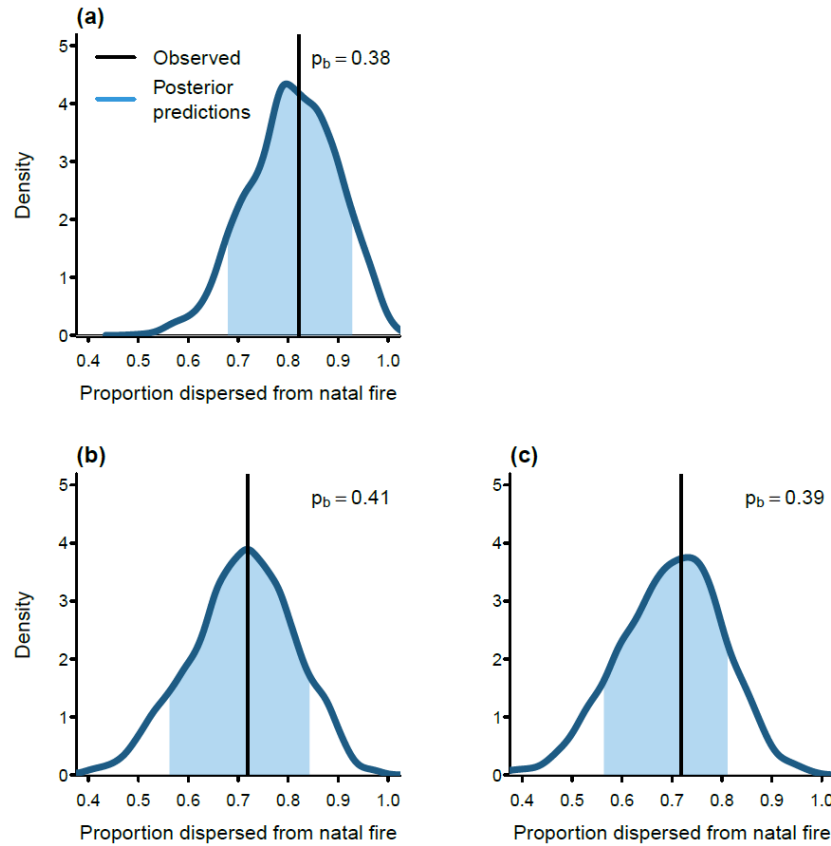


Figure S2. Posterior predictive checks indicated no evidence for lack of model fit for models of (a) fall and (b, c) spring dispersal status. We created a test statistic for each model based on the naïve proportion of individuals that dispersed from the natal fire in the fall, and the proportion of individuals that settled outside of the natal fire in the spring. In each case, we simulated test statistics from the model posterior distribution (blue line) along with 80% credible intervals (blue shading) and compared this distribution to the observed true test statistic (black line). Observed test statistics overlapping with 80% credible intervals fail to indicate a lack of fit ($p_b > 0.1$).

Chapter 5:

Molecular analysis of woodpecker diets in disturbance-prone forests

ABSTRACT

Ecological disturbance is a key agent shaping the spatial and temporal landscape of resource availability. In forests of western North America, disturbance from fire can lead to resource pulses of deadwood-associated arthropods that provide important prey for woodpeckers. Although the foraging strategies of different woodpecker species often demonstrate pronounced differences, little is known about the ways in which woodpeckers exploit and partition prey in disturbed areas. In this study, we employed DNA metabarcoding with spike-in controls to characterize and compare the arthropod diets of four woodpecker species in Washington and California, USA – Black-backed Woodpecker (*Picoides arcticus*), Hairy Woodpecker (*Dryobates villosus*), Northern Flicker (*Colaptes auratus*), and White-headed Woodpecker (*D. albolarvatus*) – primarily using nestling fecal samples from burned forests 1–13 years post-fire. Successful sequencing from 78 samples revealed the presence of over 600 operational taxonomic units (OTUs) spanning 32 arthropod orders. The diets of two species in particular – Northern Flickers and Black-backed Woodpeckers – proved to be much broader than previous observational studies would suggest. Northern Flickers demonstrated significantly higher diet richness and diversity compared to other focal species, all of which displayed considerable overlap in diet richness and diversity. Woodboring beetles, which colonize dead and dying trees after fire, were particularly important diet items for Black-backed, Hairy, and White-headed Woodpeckers. Diet composition differed between species, and diets showed limited differences between newer (≤ 5 yr) and older (> 5 yr) post-fire forests. Our results show mixed evidence for dietary resource partitioning among four woodpecker species. Three of the four focal species exhibited relatively high diet overlap, perhaps due to the pulsed subsidy of deadwood-associated arthropods in burned forests. Woodpeckers are frequently used as management indicator species

for forest health, and our study provides the first application of DNA metabarcoding to build a more complete picture of woodpecker diets.

LAY SUMMARY

- Forest disturbances such as fire create a “resource pulse” of arthropod prey for woodpeckers, yet little is known about woodpecker diets in these areas.
- We used DNA metabarcoding to characterize and compare the diets of four woodpecker species, focusing on nestling fecal samples from burned forests in the western USA.
- Woodpecker diets were broader than previous studies have reported. Northern Flicker samples showed especially high diet diversity and richness compared to other focal species.
- Black-backed, White-headed, and Hairy Woodpeckers showed a high prevalence of beetles in their diets.
- Woodpeckers are frequently used as indicators to evaluate forest management activities, and detailed characterization of woodpecker diets represents an important step in understanding their resource requirements.

INTRODUCTION

Dietary niche partitioning is an important mechanism for the coexistence of ecologically similar consumers through alleviation of resource competition (Kent & Sherry, 2020; Schoener, 1974). Partitioning among coexisting species that share morphological traits or behaviors is often expected for landscapes with a relatively consistent and predictable resource base (Kartzinel et al., 2015; Tilman, 1994). In many landscapes, however, resource availability varies widely over

space and time due to a variety of natural and anthropogenic factors. In some cases, resources may occur in a shifting mosaic where localized patches experience periods of elevated resource availability (Wimberly, 2006). Under these circumstances, characterizing predator-prey interactions and comparing diets between consumers can provide useful insights into the origin and maintenance of biodiversity in ecosystems with patchy and unpredictable resources.

Ecological disturbance is a common agent behind the changing landscape of resource availability. In forested areas, disturbances such as fire, insect outbreaks, or drought can fundamentally alter communities of consumers and their prey. After forest fire, many arthropods take advantage of regenerating vegetative growth (He et al., 2019), and deadwood-associated insects quickly colonize patches of standing, dead trees (Ray et al., 2019). As forest succession advances in the years following fire, arthropod populations change along with shifts in vegetation and deadwood availability (He et al., 2019). In temperate and boreal forests, woodpecker species arrive quickly after disturbance events to take advantage of abundant prey and nesting opportunities in dead trees (Stillman et al., 2019a; Virkkala, 2006). One species in particular, the Black-backed Woodpecker (*Picoides arcticus*), is closely associated with recently burned forests in the western USA (Hutto, 2008; Tingley et al., 2020), and observational studies suggest that they forage primarily on the larvae of woodboring beetles that live inside of dead wood (Murphy & Lehnhausen, 1998). In some cases, local woodpecker populations in recently burned areas show population trajectories that mirror the rise and fall of food availability as time since fire increases (Nappi et al., 2010; Saab et al., 2007; Tingley et al., 2018).

Because woodpecker populations respond to forest structure, woodpeckers are frequently used as indicator species to guide forest management and biodiversity conservation (Drever et al., 2008; Virkkala, 2006). Woodpeckers play a keystone role as primary cavity excavators in

forest systems, providing an important resource for other wildlife (Martin & Eadie, 1999; Tarbill et al., 2015). The specific habitat requirements of many woodpecker species make them sensitive to forest management practices that remove trees, and woodpecker populations in North America are frequently monitored to assess the ecological impact of management actions (Saab et al., 2009; Stephens et al., 2019; Tingley et al., 2020). Some species, such as Black-backed and White-headed (*Dryobates albolarvatus*) woodpeckers, are also considered species of conservation concern. Woodpeckers may also play a role in regulating outbreaks of economically-relevant arthropod pests such as bark beetles (Fayt et al. 2005). The disturbance-prone forests of western North America host a relatively high diversity of woodpecker species, yet little is known about the arthropod diets of these species or how their diets may overlap or change during resource pulses following disturbance.

Studies of woodpecker diets are conventionally conducted by carefully observing foraging or provisioning individuals (Kozma & Kroll, 2013; Murphy & Lehnhausen, 1998). While these methods can be effective at understanding general trends in prey consumption, they are highly biased towards larger prey and may not provide reliable data on prey taxonomic identity. Dissecting and identifying prey items from fecal samples can provide added taxonomic resolution, but these time-consuming methods often overlook soft-bodied prey items like larval insects (Gow et al., 2013; Pompanon et al., 2012). Advances in molecular approaches using DNA metabarcoding provide powerful tools to address these shortcomings and enhance our ability to identify taxonomic groups present in fecal material (Jedlicka et al., 2013; Pompanon et al., 2012). General, group-specific primers can be used to amplify the DNA of many prey species simultaneously, allowing fine-scale characterization of predator-prey interactions and subsequent analysis of dietary niche partitioning between sympatric consumers.

In this study, we used DNA metabarcoding to characterize and compare the diets of four woodpecker species living in disturbance-prone forests of Washington and California, USA: Black-backed Woodpecker, Hairy Woodpecker (*D. villosus*), Northern Flicker (*Colaptes auratus*), and White-headed Woodpecker (*D. albolarvatus*). Our approach used the “ANML” primer pair (Jusino et al., 2019) to amplify arthropod DNA from fecal samples and cloacal swabs primarily collected from nestlings in recently burned forests. Our objectives were to (1) describe the arthropod diet of nestlings of each species within a landscape of pulsed arthropod resources, (2) test the resource partitioning hypothesis by comparing diets between the four related species, and (3) examine whether diet composition differs in newer (≤ 5 yr post-fire) versus older (> 5 yr post-fire) burned areas, which likely witness successional changes in arthropod communities. We predicted that woodpecker diets would reflect species-specific differences in behavioral foraging strategies such as excavation, bark and foliage gleaning, and ground foraging. In addition to providing the first application of DNA metabarcoding to study the diets of woodpeckers, our study also provides new insights into the food resources consumed by two at-risk species (Black-backed Woodpecker, White-headed Woodpecker), which could be used to inform forest management practices.

MATERIALS AND METHODS

Study species and sample collection

Field observations and examinations of stomach contents have indicated that all four woodpecker species in our study primarily feed on arthropods (Beal, 1911). Consistent with their specialized habitat associations, previous work suggests that Black-backed Woodpeckers likely have a narrow diet that consists almost entirely of the larvae of woodboring beetles

(Cerambycidae and Buprestidae) which are abundant in dead and dying conifers, particularly after fire (Murphy & Lehnhausen, 1998; Villard & Beninger, 1993). In our study region, Hairy Woodpeckers and White-headed Woodpeckers forage on both dead and living trees, where they likely take advantage of a variety of bark-living insects (Kozma & Kroll, 2013; Lorenz et al., 2016). In addition, White-headed Woodpeckers are also known to forage extensively on cut stumps and live foliage in our study region (Lorenz et al., 2016). In contrast to the other three woodpeckers, Northern Flickers often forage on the ground, where ants (Formicidae) and ground beetles (Carabidae) make up important diet items (Beal, 1911; Gow et al., 2013).

We collected woodpecker samples from April to July, 2017–2018, in coniferous forests with active fire regimes in central Washington (Yakima county) and Northern California (Plumas, Lassen, and Shasta counties), USA. In Washington, sampling sites were located in mixed ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) forests of the Cascade Range. Sampling sites in California were predominantly Sierran mixed conifer forest dominated by *Pi. ponderosa*, *Pi. jeffreyi*, *Abies concolor*, *A. magnifica*, *Ps. menziesii*, and *Calocedrus decurrens*, with some sampling sites located in eastside pine forest composed of *Pi. ponderosa*, *Pi. jeffreyi*, *C. decurrens*, and *Juniperus occidentalis*. The vast majority (96%) of samples came from areas that had been burned, either by prescribed fire (53% of total) or wildfire (43% of total), within the last 13 years (mean = 5 years since fire).

We located woodpecker nests by conducting nest searches in burned areas or by tracking radio-tagged adults to nesting areas, and we monitored nests on a regular basis to predict fledging dates. Between 1–5 days before fledging, we accessed nests using the hole-saw method (Ibarzabal & Tremblay, 2006), extracted nestlings for standard in-hand processing (e.g., morphometric measurements), and immediately replaced nestlings back into the nest cavity when

processing was complete. Fresh fecal samples were collected opportunistically if a nestling defecated during the processing time or while being held in a cloth bag. In some cases, nestlings were placed in a shoebox lined with fresh white paper for up to 15 min to increase the chances of obtaining a sample. While our sampling focused on nestling woodpeckers, we also collected fecal samples opportunistically from adult or juvenile woodpeckers during behavioral observation bouts that we conducted as part of a series of separate studies (Stillman et al., 2021; Stillman et al., 2019b). In all cases, fecal samples were lifted off the substrate using a sterile cotton-tipped applicator, placed in a DNA-sterile 1.5-ml microcentrifuge tube, and stored out of direct sunlight (e.g., in a portable cooler with ice packs) until they could be transported out of the field and stored in a -18° C freezer.

In addition, we obtained 15 cloacal swab samples from nestling and adult Black-backed Woodpeckers in Washington to complement diet analysis and, if sequencing success allowed, provide information on the utility of cloacal swab samples for assessing diet. We rubbed sterile cotton-tipped applicators around the cloacal opening, placed the swabs in DNA-sterile 1.5-ml microcentrifuge tubes containing cell lysis solution (CLS; Lindner and Banik 2009), and otherwise treated them like fecal samples.

DNA extraction and sequencing

Each fecal sample was thawed at room temperature for 10 min and homogenized before extraction. Fecal DNA was extracted using the Qiagen Power Soil DNA kit according to the manufacturer's protocol (Qiagen, Germantown, Maryland) for samples preserved frozen. For cloacal swabs preserved in CLS, we extracted DNA according to the modified CLS / glass milk extraction protocol described in Jusino et al. (2016). We included negative extraction controls for both extraction methods. We then used high-throughput amplicon sequencing to identify the

dietary components. We amplified the mitochondrial gene cytochrome oxidase C subunit 1 (COI) using the ANML pair primers (Jusino et al., 2019). Forward and reverse ANML primers were modified for metabarcoding by adding Illumina Nextera adapters to each primer.

PCR reactions were performed in 15 μ L reactions using the following reagents: 7.88 μ L of DNA-free molecular grade water, 3 μ L of 5X Green GoTaq buffer (Promega, Madison, Wisconsin) for a final concentration of 1x, 3 μ L of DNA, 0.3 μ L of 10 mM dNTPs (Promega, Madison, Wisconsin) for a final concentration of 0.2 mM for each dNTP, 0.12 μ L of 20 mg/mL BSA (New England BioLabs, Ipswich, Massachusetts), 0.3 μ L of 10 mM of each primer for a final concentration of 0.2 μ M of each primer, and 0.1 μ L of 5u/ μ L GoTaq® DNA Polymerase (Promega, Madison, Wisconsin). This step included our negative extraction controls in addition to traditional PCR negative controls. Thermocycler conditions were set according to Herbert et al. (2003). PCR products were stained with SYBR Green I (Lonza Bioscience, Rockland, Maine) and run in a 2% agarose gel. Successfully amplified samples were then dual-barcoded using an eight cycle PCR reaction using the Illumina Nextera Kit.

Indexed products were visualized in a 2% agarose gel and combined by three based on band intensity. Combined samples were then cleaned and size-selected at ≤ 200 bp with Zymo Select-A-Size Clean up kits (Zymo Research, Irvine, CA) according to the manufacturer's instructions. Cleaned and size-selected products were quantified using an Invitrogen Qubit 4.0 Fluorometer and Qubit™ 1X dsDNA HS Assay kit. Then, samples were equilibrated at 3000 pM and combined. Libraries were sequenced using v3 2 \times 300 bp sequencing chemistry on the Illumina MiSeq at the University of California Riverside Institute for Integrative Genome Biology.

Bioinformatics

We bioinformatically processed our HTAS data using AMPtk version 1.4.1 (Palmer et al., 2018), available at <<http://amptk.readthedocs.io>>. We pre-processed our merged, individually barcoded reads using USEARCH (version 9.2.64) and vsearch (version 2.11.1) and then removed the forward and reverse ANML primers. We discarded any reads shorter than 170 bp. Reads longer than 181 bp were trimmed to 181 bp. Sequence reads were then quality-filtered with expected errors less than 1.0, de-replicated, and denoised using UNOISE3 (Edgar & Flyvbjerg, 2015). The resulting ASVs were then validated and clustered at 97% to generate OTUs, and sequence reads were mapped back to the resulting OTUs. The OTUs were assigned taxonomy using the hybrid taxonomy algorithm in AMPtk combined with the built-in COI database. Following taxonomy assignment, all non-arthropod OTUs were removed. We manually curated the taxonomies for all OTUs that occurred at least 5 times in our database, as well as the most frequently occurring OTUs for each woodpecker group, by comparing sequences to reference sequences in the Barcode of Life Database (BOLD) and Basic Alignment Search Tool (BLAST). OTU identification criteria for database searches followed Appendix B in Trevelline et al. (2016).

We used a single-copy equimolar arthropod mock community (Jusino et al., 2019) to parameterize our bioinformatics approach and to account for observed rates of barcode crossover using the filter module in AMPtk. This mock community was amplified, indexed, and sequenced alongside our genomic DNA products and serves as a positive community control. In addition, we repeated these methods for a single-copy equimolar question-specific mock community that we created for this study. This mock community included four beetle species which we expected to find in our diet samples: *Cypriacis aurulenta*, *Dendroctonus ponderosae*, *Monochamus scutellatus*, and *Rhagium inquisitor*.

Statistical analysis

We characterized and compared woodpecker diets using OTU presence-absence data, which reduces biases associated with using sequence read numbers as proxies for prey abundance in fecal samples (Jusino et al., 2019). Prior to analysis, we tested for differences between fecal samples and cloacal samples using PERMANOVA and Wilcoxon tests for per-sample taxonomic richness. Because both sampling methods provided a similar diet snapshot and used the same bioinformatics pipeline, we then pooled data from nestling fecal samples ($n = 66$) and nestling cloacal swabs ($n = 6$) for additional analysis. For instances where an individual had successful sequencing for both sample types, we combined presence-absence data to yield one measurement per individual. Sample size constraints prevented formal analysis of the overall utility of cloacal swab samples as a replacement for fecal samples, which we recommend as a topic for future study.

To compare diet richness and diversity between species and states, we produced rarefaction curves using the R package iNEXT (Hsieh et al., 2020). We generated interpolated estimates of diet richness, Shannon diversity (exponentiated Shannon entropy), and Simpson diversity (inverse Simpson concentration), and we used 95% confidence bands around estimates to test for differences between diets (Chao et al., 2014). Taxonomic richness estimates for each species group were rarefied to the minimum sample size ($n = 4$) and second smallest sample size ($n = 10$) to facilitate comparisons. For nestling woodpeckers only, we also compared the taxonomic richness of diet items per sample at the order- and OTU-level using two approaches. First, we tested for differences between species and states using a generalized linear model with Poisson error. Second, we tested for differences in diet taxonomic richness between recently burned areas (≤ 5 yr post-fire) and older burned areas (> 5 yr post-fire) using separate Wilcoxon

tests for each species-state group. We omitted White-headed and Hairy woodpeckers from this analysis due to inadequate sample size for within-species comparisons.

Although the true, total diets of nestmates likely have some measure of dependency due to shared parents, our samples represent single diet snapshots with substantial variation between nestmates. Therefore, we elected not to pool samples from the same nest when comparing rarefied estimates between species. Moreover, pooling nestmate samples in our study runs the risk of introducing bias when comparing richness and diversity due to species-specific differences in clutch size. In our dataset, Northern Flickers tended to have 3 times as many samples per nest compared to other species (mean samples per Northern Flicker nest = 4.0, all other species = 1.3 – 1.8). To explicitly test for potential non-independence among nestmates, we calculated the order-level dissimilarity matrix for all sample pairs within each species, decomposed to represent two dissimilarity vectors: beta diversity between nestmates and beta diversity between non-nestmates. We then compared these diversity measures using Wilcox rank sum tests.

We summarized the diet composition for each woodpecker group using two descriptive metrics: frequency of occurrence and the weighted proportion of occurrence, following equations from Deagle et al. (2019). The weighted proportion of occurrence represents a relative expression of a diet item's contribution to the whole, where each item is weighted in proportion to the number of OTUs in a sample (e.g., less weight to OTUs in a mixed meal). To test for resource partitioning in diet composition, we compared the diets of nestling woodpeckers using PERMANOVA at the OTU level (Anderson, 2001), implemented using the *adonis* function from the *vegan* package version 2.5-7 in R version 4.0.3 (Oksanen et al., 2019; R Core Team, 2020). We pooled samples by species, state, and sampling site (i.e., burned area) and included a

categorical effect for each species-state combination, a binary variable for time since fire using a threshold of ≤ 5 yr post-fire, and the interaction between both terms. In addition, we used the R package *pairwiseAdonis* to test for differences between each pair of species-state groupings. We investigated interspecific differences in multivariate dispersion between species groups, a metric of diet variability, using the *betadisper* function in the *vegan* package (Anderson, 2006; Oksanen et al., 2019). Last, we visualized dietary niche space using non-metric multidimensional scaling (NMDS). All comparisons used the modified Raup-Crick dissimilarity index.

RESULTS

We successfully recovered arthropod DNA from 66 out of 91 nestling fecal samples and 2 out of 15 adult fecal samples. We also successfully sequenced DNA from 10 out of 15 cloacal swab samples, representing 6 nestling and 4 adult Black-backed Woodpeckers. At the time of DNA extraction, samples had been stored for approximately 1.5–2.5 yr. Illumina sequencing generated 4.2 million COI sequences, which reduced to 4 million reads after quality filtering and clustered into 668 unique OTUs assigned to the Phylum Arthropoda. Of these, 662 OTUs were assigned to a taxonomic order, 197 OTUs were assigned to a family, and 131 OTUs were identified at the species level. Of the six adult woodpecker samples with successful sequencing, four cloacal swabs came from Black-backed Woodpeckers in Washington, and one fecal sample came each from a Hairy Woodpecker and (California) Black-backed Woodpecker. To avoid biased conclusions from only a single sample, we only included adult Black-backed Woodpeckers from Washington in our subsequent analysis.

Per-sample taxonomic richness for nestling Black-backed Woodpeckers from Washington did not detectably differ between swab samples ($n = 6$) and fecal samples ($n = 10$) at

the OTU level (difference in medians = 0.5, Wilcox test: $W = 30.0$, $p > 0.99$) or order-level (difference in medians = 1.5, Wilcox test: $W = 43.5$, $p = 0.15$). PERMANOVA results indicated slight differences in community composition based on sampling method, which explained 27–30% of variation at both taxonomic levels (order-level $F = 5.3$, $p = 0.05$; OTU-level $F = 6.0$, $p = 0.02$). Two Washington Black-backed Woodpecker nestlings yielded both a fecal and cloacal sample with successful sequencing, and we combined results from these samples to aid diet characterization. There were no significant differences in dissimilarity for nestmates ($n = 64$ comparisons) versus non-nestmates ($n = 507$ comparisons) in Hairy Woodpeckers, White-headed Woodpeckers, Northern Flickers, and California Black-backed Woodpeckers (Wilcox rank sum tests: $W = 4.0 - 4408.5$, $p = 0.08 - 0.91$), and many nestmates had relatively limited diet overlap (e.g., dissimilarity > 0.2). Dissimilarity values for Washington Black-backed Woodpeckers tended to be lower in nestmates versus non-nestmates (Wilcox rank sum test: $W = 181.0$, $p = 0.005$), largely due to a single nest with four samples that all contained DNA from the order Siphonaptera (e.g., fleas), despite the absence of this diet item from all but one other sample.

For our spike-in controls, we were able to recover and identify all 34 arthropods that we included in our equimolar arthropod mock community, which clustered into 32 OTUs with 268–7145 reads per OTU (mean = 1652). This mock community included two members with known sequence variants that clustered with the originating sequence (Jusino et al., 2019). Our question-specific mock community successfully recovered the four beetle species that we included and exhibited variation in read counts: *C. aurulenta* (19203), *D. ponderosae* (8577), *M. scutellatus* (1212 reads), and *R. inquisitor* (14649). This mock community also generated one additional OTU identified as *R. inquisitor* with only 62 reads.

Taxonomic richness and diversity

Dietary richness estimates were substantially higher for nestling Northern Flickers compared to other focal species – raw OTU richness was over three times greater than other woodpecker species in our study. This trend was also present at the order level, although confidence bands overlapped with nestling Hairy Woodpeckers when rarefied to the minimum sample size. Nestling Black-backed Woodpeckers had significantly lower richness estimates in Washington compared to California at both taxonomic levels, and Washington Black-backed Woodpecker samples consistently had lower richness estimates than the other three species (Table 1, Figure 1). Rarefied richness estimates were higher for adult Black-backed Woodpeckers compared to nestlings in Washington, but adults were similar to nestlings in California (Table 1).

Shannon and Simpson diversity showed a similar pattern to dietary richness when compared between nestlings from different species groups. Diversity was significantly higher for Northern Flickers compared to Black-backed Woodpeckers and White-headed Woodpeckers. Northern Flickers also had higher diversity estimates than Hairy Woodpeckers, although confidence bands overlapped at the order level. Diversity was lowest for Black-backed Woodpeckers from Washington and confidence bands did not overlap with rarefied estimates for California nestlings at the OTU level. Samples from Black-backed Woodpecker adults often had higher diversity compared to nestlings in Washington, although differences were not significant (Supplementary Material Tables S1 and S2).

Individual samples contained a median of 12 OTUs (range 1–90) and a median of 5 orders (range 1–17). Species and state (CA or WA) identity was a strong predictor of per-sample taxonomic richness at both levels and significantly reduced model deviance compared to a null model (analysis of deviance: $p < 0.001$). Nestling Black-backed Woodpecker samples from

Washington contained fewer OTUs on average compared to those from California or other species (Generalized linear model: coefficient estimates \pm sd for other groups ranged from $\beta = 0.32 \pm 0.14$ to $\beta = 1.28 \pm 0.10$, $p < 0.02$ for all groups), and Northern Flicker samples contained significantly more OTUs per sample than those from other species groups (Generalized linear model: coefficient estimates \pm sd for other groups ranged from $\beta = -0.79 \pm 0.15$ to $\beta = -1.28 \pm 0.10$, $p < 0.001$ for all groups; Figure 2). There were no meaningful differences between per-sample order richness for Black-backed, Hairy, and White-headed woodpeckers, but Northern Flicker samples contained more orders than other woodpeckers (Generalized linear model: coefficient estimates \pm sd for other groups ranged from $\beta = -0.55 \pm 0.25$ to $\beta = -0.82 \pm 0.16$, $p < 0.03$ for all groups; Figure 2). Black-backed Woodpecker samples from California had significantly greater order richness in burned areas ≤ 5 yr post-fire compared to areas > 5 yr after fire (Figure 3; Supplementary Material Table S3). Pairwise comparisons for nestling Northern Flickers and Washington Black-backed Woodpeckers did not detect meaningful differences in per-sample richness based on time since fire (Figure 3; Supplementary Material Table S3).

Diet composition

Overall, 32 orders and 68 families were detected across woodpecker samples. Coleoptera was the most frequently detected order for Black-backed, White-headed, and Hairy woodpeckers, occurring in 80–100% of samples (Table 2) and demonstrating the highest weighted percent occurrence for those species (Table 3). The most frequently detected OTUs for nestlings of these species were identified to the family Buprestidae, and in California Black-backed Woodpeckers, taxonomy of the top two OTUs was assigned to *Buprestis lyrate* and *B. laeviventris* (Supplementary Material Table S4). For the subset of samples with OTUs matched at the family level, the Coleoptera families with the highest incidence for Black-backed

Woodpeckers (n = 36) were Cerambycidae (69.4%), Buprestidae (52.8%), and Elateridae (22.2%). The most common Coleoptera families for White-headed Woodpeckers (n = 9) were Elateridae (55.6%) and Buprestidae (44.4%), and all three Hairy Woodpecker samples with family-level taxonomy contained Buprestidae. We detected DNA from bark beetles (*Dendroctonus ponderosae* and *D. valens*) in only two samples: one Hairy Woodpecker and one nestling Black-backed Woodpecker in Washington. However, woodboring beetles – here represented by Cerambycidae, Buprestidae, and Zopheridae (*Phellopsis porcata*) – occurred in the majority of samples for Black-backed, Hairy, and White-headed woodpeckers. The frequency of woodboring beetle DNA in Black-backed Woodpecker samples decreased slightly from 95% in areas ≤ 5 years after fire to 82.4% in areas > 5 years post-fire. This trend was largely driven by changes in the frequency of Cerambycidae, which decreased from 90.0% to 47.1%, and Buprestidae, which increased from 35.0% to 76.5% in newer versus older burned forests. Supplementary Table S4 summarizes the most frequent OTUs for each woodpecker species.

Prey items in the order Diptera were also frequently consumed by woodpeckers, particularly Northern Flickers (Tables 2 and 3). Northern Flicker samples showed high family-level diversity within this order – four families occurred in 2 out of 23 samples (Bibionidae, Ceratopogonidae, Muscidae, Tabanidae), while the rest occurred in only one sample each. The order Hymenoptera had the highest weighted proportion of occurrence for Northern Flickers (Table 3), and 82.6% of Northern Flicker samples contained DNA from ants in the family Formicidae. Compared to other species, White-headed Woodpeckers consumed a relatively high proportion of Hemipterans, dominated by aphids in the family Aphidae (55.6%).

The taxonomic composition of OTU-level nesting diets (pooled by species and burn site) varied significantly between species groupings (PERMANOVA $F = 5.0$, $R^2 = 0.53$, $p = 0.001$).

We did not detect differences in multivariate dispersion between species groups (ANOVA $F = 1.8$, $p = 0.17$). Pairwise comparisons between species-state groupings revealed that this variation was partially driven by differences in the diet composition of Northern Flicker nestlings compared to the other study species. California Black-backed Woodpeckers also differed from all other species groups, including Black-backed Woodpecker nestlings in Washington ($F = 3.2$, $R^2 = 0.30$, $p = 0.030$). Accounting for differences between species, we found a weak effect of time since fire on diet composition ($F = 2.6$, $R^2 = 0.07$, $p = 0.06$). NMDS ordination generated a stable 2-dimensional solution (stress = 0.155) and demonstrated divergence in diet composition between nestling Northern Flickers and other species groups (Figure 4).

DISCUSSION

Our DNA metabarcoding approach revealed the presence of over 600 OTUs representing 32 arthropod orders in the diets of four woodpecker species living in disturbance-prone forests. Woodpecker diets had greater taxonomic richness and diversity than previous studies – which have relied on observational methods – would suggest. For example, Northern Flickers are sometimes considered ant specialists, and previous diet analysis using fecal dissections suggests that over 99% of Northern Flicker diets are made up of ants (Gow et al., 2013). While we found a similarly high frequency of occurrence for the order Hymenoptera (Table 2), our results demonstrate significantly higher diet richness and diversity in Northern Flickers compared to other focal species. Along with ants, the fecal samples from Northern Flickers at our study sites frequently contained arthropods in the orders Diptera (flies), Araneae (spiders), Lepidoptera (butterflies and moths), and Coleoptera (beetles). Diet characterization using weighted proportion of occurrence suggested that rather than simply supplementing an ant-based diet,

these prey items make up a large component of Northern Flicker diets. Moreover, we found higher diet diversity in Black-backed Woodpeckers than expected based on previous studies which have emphasized the importance of woodboring beetle larvae in the diet of this species (Murphy & Lehnhausen, 1998; Villard & Beninger, 1993). While our study confirms this strong association with woodboring beetles, we were surprised by the relatively high occurrence of additional prey items in samples from this species (Tables 2 and 3). Although Black-backed Woodpeckers primarily forage by excavating into dead wood, our findings provide evidence that this species likely deviates from its typical foraging strategy to glean prey from bark, catch prey on the ground, or catch flies on the wing. Indeed, our diet diversity estimates among all four focal species suggests that woodpecker foraging behaviors are marked by a degree of foraging plasticity and opportunism (Lorenz et al., 2016).

Although sample size constraints prevented a formal analysis comparing molecular results from cloacal swab and fecal samples, our limited data show considerable overlap in diet characterization results from the two sampling techniques and suggest that under some circumstances cloacal swabs may offer a viable alternative to fecal samples when studying the diets of avian insectivores. In the field, cloacal swabs remove uncertainty associated with sample collection and can be much faster to obtain. For example, in our Washington study site only 56% of woodpeckers defecated within the time allowed by our permits for constraining birds (15 min). Cloacal swabs took less than 30 seconds and could be obtained from all birds. These observations suggest that further research comparing dietary analysis and DNA extraction from cloacal swabs and fecal samples is warranted and timely given the need to understand avian resource requirements in the face of climate and human-induced changes in arthropod prey populations (Montgomery et al., 2020).

The period of the breeding season when birds are actively provisioning altricial young is marked by high energetic demands with critical impacts on nestling survival and juvenile recruitment (Bortolotti et al., 2011; Santos & Nakagawa, 2012). In woodpeckers, nestling diets may show responses to habitat type (e.g., burned versus unburned forest; Tremblay et al., 2016), tree species composition, and even seasonal weather fluctuations (Lorenz et al., 2020). However, nestling diets could also be somewhat buffered from species-specific environmental effects due to prey selection by provisioning parents. In Black-backed Woodpeckers, provisioning rates and the size of prey deliveries tend to increase as nestlings grow older (Loverin et al. unpublished manuscript), and diet studies from marine bird species demonstrate differences between prey selected for provisioning versus prey captured for self-feeding (Alonso et al., 2012; Davoren & Burger, 1999; Ydenberg, 1994). If adult birds from different species exhibit similar prey selection when provisioning young, this raises the possibility that diets may show greater interspecific convergence among nestlings compared to adults. In burned forests, for example, different woodpecker species may take advantage of pulsed arthropod food sources in similar ways when selecting prey for nestlings but exhibit greater degrees of separation between species during the nonbreeding season, particularly if prey scarcity in the winter leads to more interspecific competition. Although sample size constraints affected our ability to test for age-specific diets, future work using DNA metabarcoding may provide insights into the potential similarities and differences between adult and nestling diets in terrestrial birds.

The advent of DNA metabarcoding has greatly enhanced our ability to investigate avian diets by reducing bias toward more conspicuous or less degradable prey (Pompanon et al., 2012). In our study, one outcome of this increased resolution was the unexpected prevalence of relatively small arthropods in nestling diets. For example, we frequently detected Diptera DNA

in samples from all four woodpecker species, including over 95% of Northern Flicker samples. Although flycatching behavior seems to be uncommon in woodpeckers (Raphael & White, 1984), our results suggest that these species may supplement their diets with aerial insects – or their larvae – on a relatively frequent basis. Another example is the high prevalence of aphids in the diet of White-headed Woodpeckers, which are known to forage on conifer cones or clusters of needles (Lorenz et al., 2016). Aphids identified to the genus *Cinara* (giant conifer aphids) occurred in 30% of White-headed Woodpecker samples and included one of the most common OTUs for this woodpecker species (Supplemental Material Table S4). Moreover, the importance of small diet items in nestling diets raises intriguing questions about provisioning behavior in the context of central-place foraging (Houston, 1985). While adults often carry larger prey items (e.g., woodboring beetle larvae) individually to nestlings (Loverin et al., unpublished manuscript), adult woodpeckers foraging on smaller prey likely need to gather multiple items in a single foraging trip. The energetic balance of these provisioning behaviors could exert considerable influence over foraging patch selection and food delivery rates (Houston, 1985).

Diet richness and composition remained similar between newer burns ≤ 5 yr and older burns > 5 yr post-fire, although PERMANOVA results indicated slight differences. Fire-killed trees gradually decay and fall as time since fire increases (Grayson et al., 2019), likely leading to declines in deadwood-associated arthropods that are important diet items for Hairy, White-headed, and Black-backed woodpeckers (Nappi et al., 2010). Despite potential changes in prey availability over time, these three woodpecker species still displayed similar nestling diets in newer and older burns. Rather than switching to alternative prey items, bark- and trunk-foraging woodpeckers may instead demonstrate numerical responses to time since fire that track resource availability. For example, post-fire population trajectories tracking the pulse and decline of post-

fire resources have already been documented in Hairy and Black-backed woodpeckers (Saab et al., 2007; Tingley et al., 2018). In comparison to these species, Northern Flicker nestlings in our study had high diet diversity, and samples showed a low prevalence of deadwood-associated beetles (Table 2, 3). It is possible that high diet diversity, combined with a ground-based foraging strategy in open areas, may allow Northern Flickers to maintain stable or increasing populations in the decade following forest fire (Wiebe, 2014). In western Idaho, for example, Saab et al. (2007) found that Northern Flicker nest densities increased between 1–10 years post-fire.

While our results support the hypothesis that Northern Flickers occupy a distinct dietary niche in post-fire landscapes compared to other focal species, we observed more overlap in diet richness and diversity than expected among Hairy, Black-backed, and White-headed woodpeckers. Under the resource partitioning hypothesis, we predicted that these three sympatric species would demonstrate divergence in diet characteristics in response to interspecific competition for food resources (Schoener, 1974). However, the diets of species with different foraging strategies have been shown to converge in times of high food supply, such as abundant ants for overwintering migrants (Kent & Sherry, 2020), or seasonally emergent aquatic insects in riparian habitats (Trevelline et al., 2018). Our samples primarily came from burned forests in Washington and California, where abundant fire-killed trees produce a resource pulse of deadwood-associated insects (Costello et al., 2011; Ray et al., 2019). Thus, our observed diet similarities between Black-backed, White-headed, and Hairy woodpeckers – which usually exhibit different foraging strategies – may represent a case of diet convergence during opportunistic foraging in the presence of a pulsed food source. If this is the case, sympatric woodpecker species should show greater diet divergence in unburned forest compared to burned

forest, although this prediction has not been tested. Ecological disturbances such as forest fire create complex landscapes of resource availability with cascading effects on the community structure of sympatric consumers (He et al., 2019). Our results highlight the utility of molecular tools for characterizing avian diets in order to test predictions about resource partitioning among insectivores living in this dynamic landscape.

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Ethics statement

Field methods were approved by the University of Connecticut Institutional Animal Care and Use Committee (Protocol #A16-008), the USFS Animal Care and Use Committee (2016-007), the California Department of Fish and Wildlife (Scientific Collecting Permit #SC-8645), the Washington Department of Fish and Wildlife, and the USFWS Bird Banding Laboratory (Permits 22423, 24061).

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Table 1. Number of sequenced samples, raw diet richness, and rarefied diet richness estimates for four woodpecker species in Washington and/or California, USA. Taxonomic richness estimates for each species group were rarefied to the minimum sample size (n = 4) and second smallest sample size (n = 10) to facilitate comparisons. Rarefied numbers give the mean estimate along with 95% confidence intervals in parentheses.

Species group	Samples	OTU level			Order level		
		Raw richness	Interpolated (n = 4)	Interpolated (n = 10)	Raw richness	Interpolated (n = 4)	Interpolated (n = 10)
<i>Nestlings</i>							
Black-backed Woodpecker (California)	18	126	38.2 (33.7, 42.7)	81.6 (72.6, 90.6)	16	9.3 (7.7, 10.9)	13.5 (11.2, 15.8)
Black-backed Woodpecker (Washington)	14	74	27.5 (23.2, 31.8)	57.7 (48.8, 66.5)	10	6.7 (5.6, 7.7)	9.1 (7.1, 11.0)
Hairy Woodpecker (Washington)	4	43	43.0 (31.3, 54.7)	----	10	10.0 (6.1, 13.9)	----
Northern Flicker (Washington)	24	396	98.6 (92.3, 104.9)	207.4 (194.5, 220.3)	29	14.1 (12.2, 16.1)	20.3 (16.5, 24.1)
White-headed Woodpecker (Washington)	10	82	38.7 (33.7, 43.7)	82 (71.1, 92.9)	12	8.8 (6.9, 10.7)	12.0 (8.8, 15.2)
<i>Adults</i>							
Black-backed Woodpecker (Washington)	4	41	41 (30.7, 51.3)	----	9	9.0 (6.3, 11.7)	----

Table 2. Frequency of occurrence (%) of prey orders identified in the diets of four focal woodpecker species, presented separately by study region (California vs. Washington) and/or age (nestling vs. adult). Data are shown for the 15 orders with highest overall frequency.

Order	<i>Nestlings</i>					<i>Adults</i>
	n = 18	n = 14	n = 4	n = 24	n = 10	n = 4
	Black-backed Woodpecker (CA)	Black-backed Woodpecker (WA)	Hairy Woodpecker (WA)	Northern Flicker (WA)	White-headed Woodpecker (WA)	Black-backed Woodpecker (WA)
Coleoptera	94.4	92.9	100	62.5	80	100
Diptera	38.9	78.6	50	95.8	50	75
Araneae	38.9	35.7	75	83.3	40	100
Hymenoptera	50	21.4	25	95.8	50	50
Lepidoptera	44.4	35.7	50	83.3	30	50
Hemiptera	11.1	0	25	66.7	70	25
Entomobryomorpha	16.7	7.1	0	29.2	10	25
Sarcoptiformes	0	0	0	50	0	0
Trichoptera	22.2	7.1	0	20.8	20	0
Diplostraca	11.1	0	0	29.2	0	0
Isopoda	16.7	14.3	0	4.2	30	0
Ephemeroptera	0	0	0	25	0	25
Trombidiformes	5.6	7.1	0	20.8	0	0
Blattodea	27.8	0	0	4.2	0	0
Siphonaptera	0	35.7	25	0	0	0

Table 3. Weighted proportion of occurrence of prey orders identified in the diets of four focal woodpecker species, presented separately by study region (California vs. Washington) and/or age (nestling vs. adult). Data are shown for the 15 orders with highest overall frequency. Values sum to 1 for each species group (when all orders are included).

Order	<i>Nestlings</i>					<i>Adults</i>
	n = 18	n = 14	n = 4	n = 24	n = 10	n = 4
	Black-backed Woodpecker (CA)	Black-backed Woodpecker (WA)	Hairy Woodpecker (WA)	Northern Flicker (WA)	White-headed Woodpecker (WA)	Black-backed Woodpecker (WA)
Coleoptera	0.5	0.41	0.67	0.04	0.27	0.38
Diptera	0.1	0.19	0.12	0.24	0.1	0.18
Araneae	0.08	0.05	0.05	0.11	0.04	0.28
Hymenoptera	0.09	0.05	0.05	0.31	0.19	0.04
Lepidoptera	0.05	0.06	0.04	0.14	0.04	0.04
Hemiptera	0	0	0.01	0.05	0.26	0.02
Entomobryomorpha	0.03	0.01	0	0.01	0.01	0.02
Sarcoptiformes	0	0	0	0.02	0	0
Trichoptera	0.02	0	0	0.01	0.03	0
Diplostraca	0.01	0	0	0.01	0	0
Isopoda	0.01	0.02	0	0	0.04	0
Ephemeroptera	0	0	0	0.01	0	0.02
Trombidiformes	0	0.01	0	0.01	0	0
Blattodea	0.1	0	0	0	0	0
Siphonaptera	0	0.19	0.01	0	0	0

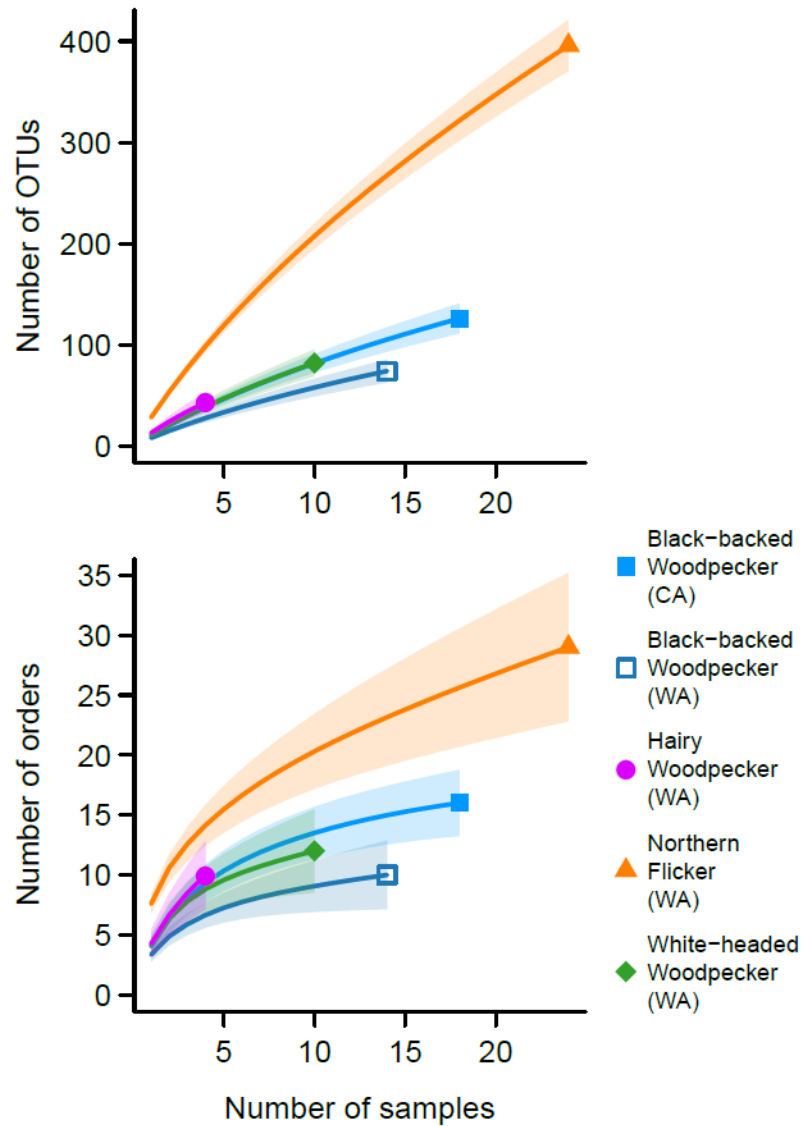


Figure 1. Rarefaction curves for the number of OTUs (top) and taxonomic orders (bottom) identified in the diets of nestling woodpeckers. Points indicate observed diet richness at the true sample size for each species, and shaded regions show 95% confidence intervals. Samples were analyzed separately, where applicable, depending on study region (California vs. Washington).

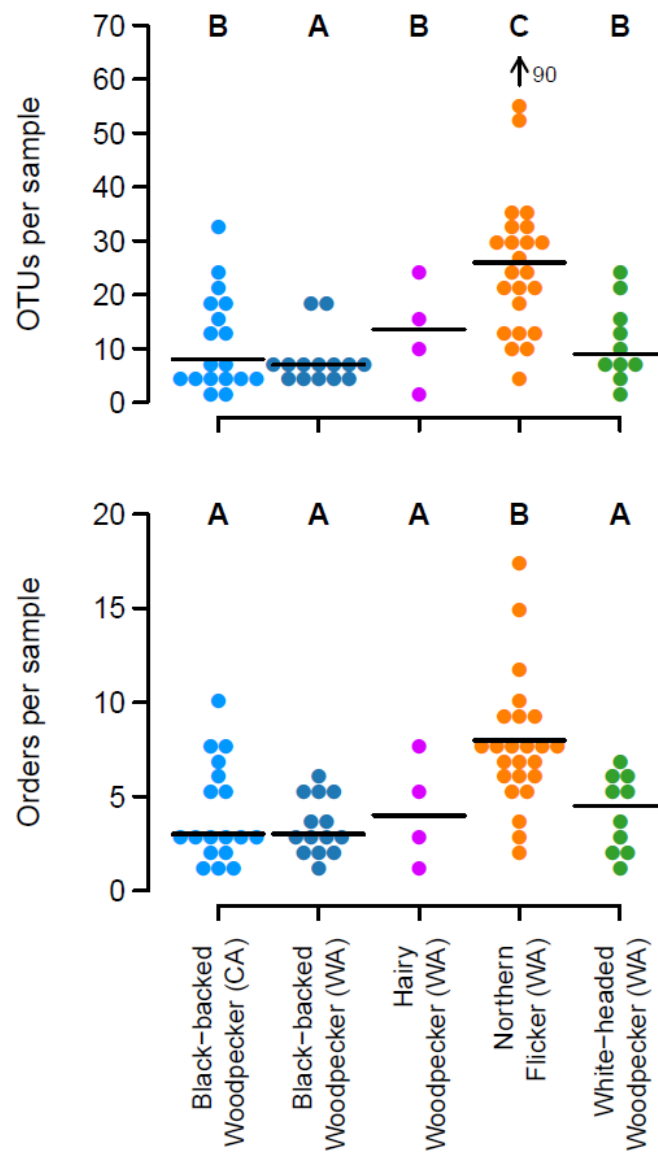


Figure 2. Per-sample dietary richness for four woodpecker species at the level of OTUs and taxonomic orders. Each point represents a nestling, black lines show the median value, and the arrow (top) gives the value of an outlier. Letters represent groupings that are significantly different from each other ($p < 0.05$) based on a generalized linear model. Samples were analyzed separately, where applicable, depending on study region (California vs. Washington).

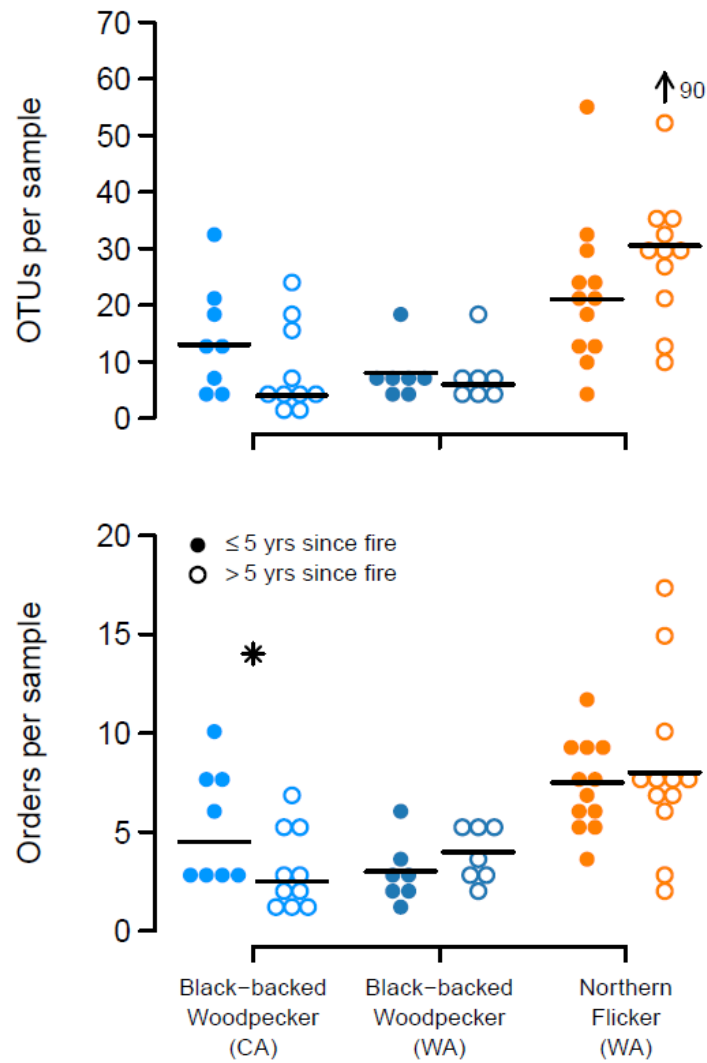


Figure 3. Per-sample dietary richness for nestling black-backed woodpeckers and northern flickers, divided based on years since fire at the sampling site. Each point represents an individual, black lines show the median value, and the arrow (top) gives the value of an outlier. Pairs that are significantly different from each other ($p < 0.05$) are marked with an asterisk.

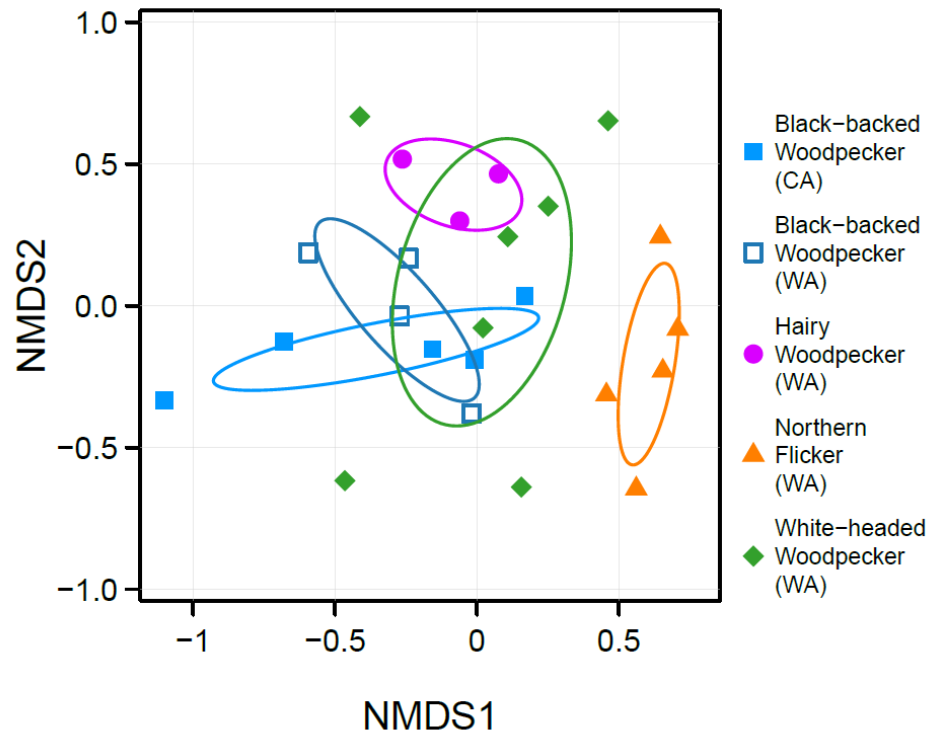


Figure 4. NMDS ordination of nestling diet composition for four species of woodpeckers. Points represent diet composition based on OTUs, pooled for each species and sampling site (i.e., burned area) combination. Ovals indicate 95% confidence intervals around the spatial median for each species and state. Samples were analyzed separately, where applicable, depending on study region.

Supplemental Material

Table S1. Rarefied estimates of Shannon diversity (exponentiated Shannon entropy) for four woodpecker species in Washington and California, USA. Taxonomic diversity estimates for each species group were rarefied to the minimum sample size ($n = 4$) and second smallest sample size ($n = 10$) to facilitate comparisons. Rarefied numbers give the mean estimate along with 95% confidence intervals in parentheses.

Species group	Samples	OTU level		Order level	
		Interpolated (n = 4)	Interpolated (n = 10)	Interpolated (n = 4)	Interpolated (n = 10)
<i>Nestlings</i>					
Black-backed Woodpecker (California)	18	36.7 (31.4, 41.9)	73.4 (63.5, 83.2)	8.1 (7.0, 9.2)	10.3 (8.8, 11.8)
Black-backed Woodpecker (Washington)	14	26.3 (22.6, 30.0)	51.1 (41.9, 60.3)	5.7 (4.6, 6.9)	6.9 (5.5, 8.2)
Hairy Woodpecker (Washington)	4	40.6 (31.3, 49.9)	----	8.6 (5.7, 11.5)	----
Northern Flicker (Washington)	24	94.0 (89.3, 98.7)	182.2 (169.6, 194.8)	12.1 (10.9, 13.4)	14.4 (12.7, 16.2)
White-headed Woodpecker (Washington)	10	37.3 (31.6, 43.1)	74.6 (61.4, 87.7)	7.8 (6.4, 9.2)	9.5 (7, 12)
<i>Adults</i>					
Black-backed Woodpecker (Washington)	4	37.6 (27.6, 47.5)	----	7.6 (5.5, 9.7)	----

Table S2. Rarefied estimates of Simpson diversity (inverse Simpson concentration) for four woodpecker species in Washington and California, USA. Taxonomic diversity estimates for each species group were rarefied to the minimum sample size (n = 4) and second smallest sample size (n = 10) to facilitate comparisons. Rarefied numbers give the mean estimate along with 95% confidence intervals in parentheses.

Species group	Samples	OTU level		Order level	
		Interpolated (n = 4)	Interpolated (n = 10)	Interpolated (n = 4)	Interpolated (n = 10)
<i>Nestlings</i>					
Black-backed Woodpecker (California)	18	34.6 (30.7, 38.5)	63.1 (55.9, 70.3)	7.1 (5.7, 8.4)	8.3 (6.7, 9.9)
Black-backed Woodpecker (Washington)	14	24.7 (20.7, 28.7)	43.6 (35, 52.1)	5.1 (4.2, 6)	5.7 (4.6, 6.7)
Hairy Woodpecker (Washington)	4	37.7 (28.2, 47.2)	----	7.4 (4.9, 9.9)	----
Northern Flicker (Washington)	24	87.7 (80.4, 95)	152.7 (136.8, 168.7)	10.8 (9.6, 12)	11.8 (10.4, 13.2)
White-headed Woodpecker (Washington)	10	35.5 (29.4, 41.6)	66.2 (54.3, 78.1)	7.0 (5.7, 8.4)	8.2 (6.4, 10)
<i>Adults</i>					
Black-backed Woodpecker (Washington)	4	32.9 (23.2, 42.6)	----	6.7 (4.9, 8.5)	----

Table S3. Results from Wilcoxon ranked sum tests for differences in per-sample taxonomic richness between recently burned areas (≤ 5 yr post-fire) and older burned areas (> 5 yr post-fire). Tests were performed separately for each nestling species at two taxonomic levels.

Nestling species	n*	<i>OTU level</i>		<i>Order level</i>	
		W	p	W	P
Black-backed Woodpecker (CA)	8, 10	57.5	0.130	63.0	0.041
Black-backed Woodpecker (WA)	7, 7	27.0	0.793	15.5	0.267
Northern Flicker (WA)	12, 12	42.5	0.094	66.0	0.748

* number of samples ≤ 5 years post-fire, number of samples > 5 years post-fire.

Table S4. Frequency of occurrence and taxonomic identification for the most common OTUs in samples from nestling woodpeckers of four species and adult Black-backed Woodpeckers. Taxonomy was assigned using the AMPtk pipeline with additional curation using reference sequences in the Barcode of Life Database (BOLD) and Basic Alignment Search Tool (BLAST). OTU identification criteria for database searches followed Trevelline et al. (2016 Appendix B).

Woodpecker species*	OTU ID	Freq. of Occurrence	Taxonomy
Black-backed Woodpecker (California)	OTU7	50	Insecta, Coleoptera, Buprestidae, <i>Buprestis lyrata</i>
	OTU1617	27.8	Insecta, Coleoptera, Buprestidae, <i>Buprestis laeviventris</i>
	OTU2	22.2	Insecta, Coleoptera, Elateridae, <i>Hadromorphus callidus</i>
	OTU11	22.2	Insecta, Blattodea, Archotermopsidae, <i>Zootermopsis nevadensis</i>
	OTU113	22.2	Insecta, Coleoptera, Cerambycidae, <i>Rhagium inquisitor</i>
	OTU303	22.2	Arachnida, Araneae, Amaurobiidae, <i>Callobius nomeus</i>
	OTU866	22.2	Insecta, Diptera, Tachinidae
	OTU17	16.7	Insecta, Coleoptera, Buprestidae
	OTU59	16.7	Insecta, Coleoptera, Cerambycidae, <i>Monochamus notatus</i>
	OTU19	16.7	Insecta, Coleoptera, Cerambycidae, <i>Acanthocinus princeps</i>
	OTU27	16.7	Collembola, Entomobryomorpha
	OTU673	16.7	Insecta, Coleoptera, Buprestidae, <i>Buprestis lineata</i>
	OTU1162	16.7	Insecta, Coleoptera, Buprestidae, <i>Buprestis</i> sp.
	OTU1657	16.7	Insecta, Coleoptera, Cerambycidae, <i>Rhagium inquisitor</i>
	OTU1719	16.7	Insecta, Coleoptera
	OTU1568	16.7	Arachnida, Araneae, Amaurobiidae, <i>Callobius nomeus</i>
Black-backed Woodpecker (Washington)	OTU17	42.9	Insecta, Coleoptera, Buprestidae
	OTU13	35.7	Insecta, Coleoptera, Cerambycidae, <i>Acanthocinus obliquus</i>
	OTU5	28.6	Insecta, Siphonaptera, Ceratophyllus
	OTU34	28.6	Insecta, Diptera, Psychodidae, <i>Pressatia choti</i>

	OTU113	28.6	Insecta, Coleoptera, Cerambycidae, <i>Rhagium inquisitor</i>
	OTU809	21.4	Insecta, Siphonaptera, Ceratophyllidae, <i>Ceratophyllus sp.</i>
	OTU759	21.4	Insecta, Coleoptera, Cerambycidae, <i>Ortholeptura valida</i>
Hairy Woodpecker (Washington)	OTU17	75	Insecta, Coleoptera, Buprestidae
	OTU59	50	Insecta, Coleoptera, Cerambycidae, <i>Monochamus sp.</i>
	OTU87	50	Arachnida, Araneae, Amaurobiidae, <i>Callobius bennetti</i>
	OTU38	50	Insecta, Coleoptera
	OTU267	50	Diplopoda, Julida
	OTU984	50	Insecta, Coleoptera, Throscidae, <i>Trixagus meyhohmi</i>
	OTU1097	50	Insecta, Diptera, Tachinidae, <i>Billaea nipigonensis</i>
Northern Flicker (Washington)	OTU14	45.8	Insecta, Hymenoptera, Formicidae, <i>Myrmica detritinodis</i>
	OTU1779	45.8	Insecta, Hymenoptera, Formicidae, <i>Myrmica detritinodis</i>
	OTU8	41.7	Insecta, Hymenoptera
	OTU42	37.5	Insecta, Hymenoptera, Formicidae, <i>Formica lasioides</i>
	OTU128	37.5	Insecta, Lepidoptera, Noctuidae, <i>Euxoa sp.</i>
	OTU65	37.5	Insecta, Diptera, Cecidomyiidae
	OTU22	33.3	Arachnida, Araneae
	OTU131	33.3	Insecta, Hemiptera
	OTU74	25	Insecta, Diptera
	OTU156	25	Insecta, Hymenoptera, Formicidae, <i>Myrmica cf. fracticornis</i>
	OTU171	25	Insecta, Hymenoptera
	OTU144	25	Insecta, Diptera
	OTU569	25	Insecta, Hymenoptera, Formicidae, <i>Myrmica cf. fracticornis</i>
	OTU521	25	Insecta, Diptera
	OTU1669	25	Insecta, Hymenoptera, Formicidae, <i>Myrmica cf. fracticornis</i>

	OTU718	25	Insecta, Lepidoptera, Noctuidae, <i>Euxoa satis</i>
White-headed Woodpecker (Washington)	OTU17	40	Insecta, Coleoptera, Buprestidae
	OTU4	30	Malacostraca, Isopoda
	OTU56	30	Insecta, Hymenoptera, Formicidae, <i>Camponotus sp.</i>
	OTU307	30	Insecta, Hemiptera, Aphididae, <i>Cinara pseudotaxifoliae</i>
	OTU984	30	Insecta, Coleoptera, Throscidae, <i>Trixagus meyhohmi</i>
	OTU1470	30	Insecta, Coleoptera, Buprestidae
Adult Black-backed Woodpecker (Washington)	OTU59	100	Insecta, Coleoptera, Cerambycidae, <i>Monochamus sp.</i>
	OTU87	75	Arachnida, Araneae, Amaurobiidae, <i>Callobius bennetti</i>
	OTU13	50	Insecta, Coleoptera, Cerambycidae, <i>Acanthocinus obliquus</i>
	OTU303	50	Arachnida, Araneae, Amaurobiidae, <i>Callobius nomeus</i>
	OTU1721	50	Insecta, Coleoptera, Cerambycidae, <i>Monochamus sp.</i>

* OTUs shown in this table have a frequency of occurrence greater than or equal to 3/18 for California Black-backed Woodpeckers, 3/14 for Washington Black-backed Woodpeckers, 2/4 for Hairy Woodpeckers, 6/24 for Northern Flickers, 3/10 for White-headed Woodpeckers, and 2/4 for adult Black-backed Woodpeckers.